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This Journal, which was founded in 1913 as the organ of The British Ecological Society, was the first periodical devoted exclusively to ecology. It contains original contributions to general and plant ecology, and to *The Biological Flora of the British Isles*, reviews, and reports of the meetings of the British Ecological Society.

Three issues of the Journal appear each year together making a volume of about 800 pages. The current subscription price to non-members of the Society is 84*s*. per volume, single parts 35*s*. net. Back volumes are available at 70*s*. each.

BLACKWELL SCIENTIFIC PUBLICATIONS

ECOLOGY AS AN EXPERIMENTAL SCIENCE

By G. C. VARLEY

(*Hope Department of Entomology, Oxford*)

(BEING THE PRESIDENTIAL ADDRESS TO THE BRITISH ECOLOGICAL SOCIETY DELIVERED ON 8 JANUARY 1957)

My choice of the subject for this address was largely influenced by the excellent summer meeting held by this society at the Ferry House laboratory of the Freshwater Biological Association, and our visit to the Nature Conservancy's laboratory at Merlewood. Subsequently I received from Wellington, New Zealand, the gift of a duplicate copy of the first part of the *Journal of Ecology*, which was the first publication of this Society. There you will find a long and critical review by A. G. Tansley of Brockmann-Jerosch and Rübel's universal classification of plant communities, from which I would like to quote the following exhortation (p. 42): 'We must strive by comparison, by observation and experiment to elucidate those features of the habitat which determine the vegetation . . . Only on those lines can we establish a real "inductive" system, which we are at present very far from having attained.' This is still true today, to a considerable extent because ecologists have confined themselves too rigidly to observation and comparison, and have used experimental methods too little. I wish in this address to point to some studies which seem to me to lead to exciting new possibilities, which can quickly be exploited experimentally.

Unfortunately the major ecological experiments, or shall we say experiments with ecological effects, are not being performed by ecologists, and in many cases are not even being observed by ecologists. Every year new areas of the world are brought into agricultural use, and either crops are sown, or stock is introduced. This either at once destroys much of the natural vegetation, or greatly influences it. All too often overgrazing leads to soil erosion and permanent impoverishment of the land. Settlers in new continents unintentionally introduce weeds, or plants are introduced on purpose as ornamentals in gardens and then may escape and compete successfully with native plants.

Introduced birds like the European house sparrow and the starling in the North American continent have had even more spectacular successes. Rabbits, goats, pigs and foxes and other mammals have been introduced to many new islands and continents, and even in Great Britain some of our most familiar mammals, like the rabbit, grey squirrel and rats, have been introduced, and a number less well known like the fat dormouse and coypu are spreading; many of our household pests, like cockroaches, pharaoh's ant, the silver fish and fire brat, to say nothing of many of our serious pests of stored products, have been introduced from warmer climates.

Foresters have planted large areas of the country with native or even exotic trees. Forests, orchards and field crops threatened with damage by insect pests are sprayed or dusted with insecticides, with unknown effects on other creatures over a wide area. Exotic food fish like the African *Tilapia* have been introduced into lakes and streams in Malaya and many other parts of the tropical world, as a foundation for commercial fisheries. The European carp in South Africa is now causing considerable concern because it feeds in the mud, and so disturbs the bottoms of rivers as to alter their nature. To provide sport, brown and rainbow trout have been introduced into suitable streams all over the world. The canal by-passing the Niagara Falls has allowed the sea lamprey to enter the Great Lakes where it is greatly affecting the commercial and sporting fisheries. Our growing towns require more and more water. Head streams are diverted, and water is stored in large reservoirs. The flow in our rivers is reduced and regulated, and quantities of chemical effluent, and sewage (more or less treated) are poured in. Then power stations warm up the resulting soup, and increase the oxygen demand of the aerobic bacteria, until the waters become too deficient in oxygen for the normal animals and plants to survive.

Even in continents such as Africa, where the population is sparse, from time immemorial the natives have used fire to clear the land. Where *Simulium damnosum* transmits the worm *Onchocerca* which causes human blindness, medical entomologists have attacked the fly by putting DDT into the rivers. To control the tsetse flies which transmit trypanosomiasis to man and domestic animals in Africa, large areas of riverine thickets have been cleared to eliminate the habitat of certain species; in other areas there has been wholesale destruction of the game which provided a reservoir for the trypanosome.

To combat yellow fever and malaria the swamps in which mosquitoes breed have been drained, and other areas have been treated with insecticides. Even the oceans are not immune from overfishing, and the whaling industry has to be carefully supervised to prevent in the antarctic seas the extinction of the whales, already almost complete in the North Atlantic. The continental shelves are already overfished in many regions and the offal from the large catches is thrown back with considerable effect on the seabird population. On the other hand many seabirds are destroyed every year by the oil thrown out by ships at sea. Ships in harbour become invaded by sedentary organisms which are then transported all over the world. Some, like the barnacle *Elminius* and the slipper limpet *Crepidula*, have become locally abundant round our coasts. The waste heat from power stations may so warm the waters of British harbours that new forms such as the ship worm *Teredo* can multiply, and may possibly become a danger.

Although ecologists may have helped to initiate some of the changes mentioned here, most have taken place without even being observed by ecologists. None has been followed up in detail. We have thus failed to learn the ecological lessons that they might have taught us. Whilst such vast experiments are taking place it is disturbing to find ecologists seeking remote places where they can study 'natural habitats', i.e. those least obviously changed by man. This kind of work in distant places tends to be so expensive in travel that visits are too few and too short for the work to develop beyond a superficial and descriptive stage. If ecology is to play a part in the world, and in nature conservation, ecologists must not hold themselves aloof. They must instead learn to use and understand experimental methods which provide the most powerful tools in scientific analysis, and use them to investigate the basic principles of ecology, which operate on animals and plants everywhere.

An understanding of the ecology of our fauna and flora requires knowledge of the interactions between the animals and the plants, as well as between each species and its physical environment. We need to study not only the physiology of the plants and animals but also their behaviour. Physiology and behaviour tend to be neglected by ecologists, but are in my opinion basic to our science. Those who know the Association for the Study of Animal Behaviour will agree that many topics of the greatest ecological importance are discussed at their meetings. The series of wonderful monographs by the late Prof. P. A. Buxton and members of his school, on the louse, tsetse flies and mosquito behaviour (by R. C. Muirhead-Thompson) combine fascinating physiological and behaviour studies in which experimental methods have been used in a multiplicity of ways to aid the understanding of the ecology of these animals.

However, in spite of the vast and successful effort put into the studies of these animals of medical importance, the ecology of birds is even more advanced. This illustrates how basic scientific problems tend to be solved most easily with material that is particularly favourable. Birds can be identified in the field more readily than any other animals; being diurnal, territorial and oviparous, they can be counted and studied with comparative ease, and the fascinating studies available in book form on the robin, the heron, the fulmar and the swift, to mention but a few, have no counterpart in botanical literature. David Lack has recently synthesized the population work on birds and other animals in his admirable book *The Natural Regulation of Animal Numbers*. He starts from the viewpoint so well expressed by Darwin in the third chapter of *The Origin of Species*, and seeks and finds adaptive significance in what animals do. He reaches the conclusion that populations are likely to be regulated by a complex combination of food limitation, predation and disease, rather than by any one factor alone.

In studying the population ecology of insects I have found theoretical studies of enormous help in planning the research and in the analysis of results. Not only can a theory be a guide to thought, but it may suggest directions in which solutions to basic problems may be sought. A clear formulation of an ecological problem can lead to the recognition of favourable material upon which it may be particularly easy to make the observations needed for a proper understanding.

In theoretical papers, Nicholson (1933) and Nicholson and Bailey (1935) have laid a foundation for the study of the interaction of parasitic insects and their hosts, and recently Nicholson (1954) has generalized this theory and considered some of its wider applications. For him populations are self-governing systems, which regulate population densities by depleting 'requisites' up to the limits of unfavourability. This is very close to the much older idea of limiting factors.

The mechanism of 'population density governance' of a species is, according to Nicholson (1954), almost always intraspecific competition either for 'transient requisites' such as light, or 'accumulative requisites' such as chemical nutrients, or 'reproductive requisites' such as a food-providing organism. Alternatively the species may be governed by the attack of a predator, parasite or disease organism, in which case it is this second species which is limited by the availability of the first, which is, for it, a reproductive requisite. We can construct a simple energy- or food-chain, in which light energy is used by a plant that is in turn eaten by an insect, with parasitic and hyperparasitic species. Each link in the chain is of course influenced by the physical environment. In this model, the numbers of individuals of alternate species in the energy chain will be controlled by the mortality caused by the next species. If the hyperparasite is efficient, and maintains the population density of the parasite at a low level, this leaves the phytophagous insect to increase until it reduces the plant population to a low level, at which the insect is at the starvation level. The plant will then be rare, and other plants will 'compete' successfully with it. On the other hand, if the hyperparasite is inefficient or absent, the parasite can keep the population of the phytophagous insect at a low level, and the plant may then increase until it is up against the limit of light, water, or nutrients. Such a plant is 'dominant' in its association.

Obviously this model is oversimplified, but it provides the basis for our understanding of the successful biological control of insect pests or of weeds, such as for instance the prickly pear (*Opuntia*) in Australia by the introduction of the moth *Cactoblastis* and St. John's Wort (*Hypericum*) in California by introducing the plant feeding beetle *Chrysolina*. The European click-beetle *Agriotes sputator* (L.) introduced into Canada lacks efficient predators there, and by feeding on grass roots its wireworm larvae have ruined good pasture land, which has come to be dominated by *Hieracium* species, which the larvae do not like to eat (Fox and MacLellan, 1956). To consider either plant or animal sociology separately cannot lead to a sound understanding of ecological problems.

However, a simple model has, I maintain, the virtue that it helps us to pose simple questions which can be studied by properly planned observations, or experimentally. To explain why a species is common or rare requires a study of its reproductive rate and the mortality due to all causes up to the next reproductive stage. It is only too seldom that ecologists have measured reproductive rates and death rates in animals, or seed production, dispersal, germination, establishment and growth in plants.

Some of you may have wondered why I have so far avoided using the term 'density dependent factor'. The term was first used and defined by H. S. Smith (1935) as a synonym of Howard and Fiske's 'facultative agencies'. These kill a higher proportion of the population when the population density is high, and have been thought to be responsible for population balance or natural control. At the same time Smith renamed their 'catastrophic agencies' and called them 'density independent factors'. The latter kill a proportion which is unaffected by population density. From the start there was confusion because Howard and Fiske, Smith and Nicholson (1933) mistakenly assumed that parasitic insects acted as density dependent mortality factors on their hosts. There is no reliable evidence from behaviour studies that parasites act precisely in this way, nor in fact do the theoretical studies of either W. R. Thompson or Nicholson (1954) suggest that they should be expected to behave as density dependent factors as this term has been defined. This is not to deny that they have an important influence on animal and indirectly on plant populations.

More recently confusion has increased because some authors have misunderstood the terms and used them wrongly, and others have purposely used Smith's terms in different, or even opposite senses to the original. Neither of these courses can lead to anything but chaos.

The diagram (Fig. 1) will clarify this (see also Varley, 1953). Curves A_1, A_2 and A_3, although by no means identical, all show relationships which equally fit Howard and Fiske's definition of facultative agencies, controlling agencies (Nicholson, 1933) density dependent factors (Smith, 1935; Odum, 1954, etc.), density governing factors (Nicholson, 1954). Haldane (1953) with perverse logic has used the term 'negative density dependent factor' as a synonym.

Straight lines like B represent Howard and Fiske's catastrophic agencies, which are Smith's density independent factors. Odum (1954) calls them density proportional factors. Ullyett (1947) found this relationship between mortality and population density for the diamond back moth, and wrongly called it density dependent.

The possibility of relationships like C was recognized by Smith, but not named. Nicholson (1954) called factors producing this effect density disturbing factors, but

Haldane (loc. cit.) called them density dependent. Included in C is the special case where a fixed number is killed at all population densities. Odum (loc. cit.) called these density independent factors.

On reading either Nicholson (1933) or Smith (1935) it might wrongly be supposed that the mortality due to a parasite or predator could be represented adequately by some curve of type A, and often parasites are claimed to act as density dependent factors of mortality on their hosts. I pointed out (Varley, 1948, 1953) that Nicholson's calculations suggest that the entirely different relationship D is to be expected for the mortality caused by either parasites or predators in successive generations of a host. Furthermore if the ordinate of Fig. 1 represents the rate of increase of a parasitic or predatory species, and the abscissa its population density in successive generations, then the points on curve D show the form of the relationship between them. Food or host supply here is acting as a reproductive requisite (Nicholson, 1954) which limits increase. It acts as a delayed density dependent factor (Varley, 1948) and the population densities of both species show oscillations. Only if food supply is a persistent or transitory requisite (Nicholson, 1954) will it act as a density dependent factor (Smith, 1935) and then the population density curve against time will be of the Pearl-Verhulst type. Let us hope that this confused and confusing subject will eventually be clarified. Meanwhile it remains as a terrible example of the way in which a good idea, and a useful term, can by careless misuse be rendered almost valueless. Should there not be a rule of priority of definition, comparable to those governing zoological and botanical nomenclature, to protect proper usage?

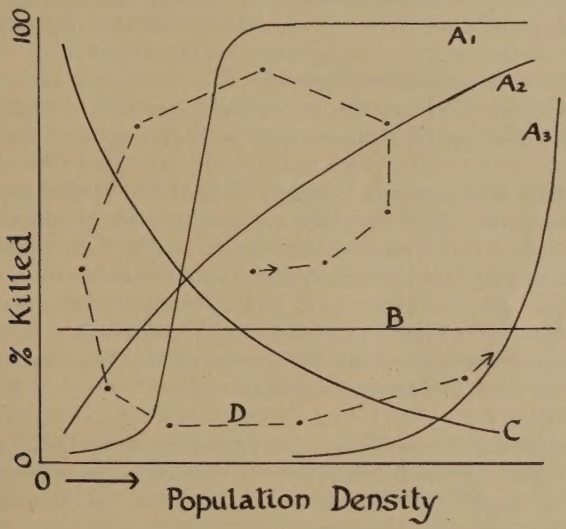

Fig. 1. Relationships between mortality and population density of organisms:
A_1, A_2, A_3: Density dependent mortality (Smith, 1935)
B: Density independent mortality (Smith, 1935)
C: Density disturbing mortality (Nicholson, 1954)
D: Delayed density dependent mortality (Varley, 1948). The percentages killed by specific parasites or predators in successive generations are joined serially by a pecked line. If the ordinate represents the number of parasite or predator progeny per female in each generation, the points on the curve D show the delayed density dependent relationship with parasite or predator population density.

A further difficulty is inherent in this classification of different types of mortality relationships. Density dependent and density disturbing factors are defined positively, but density independency is the limiting case between them. One might expect it to be difficult to distinguish a small change in mortality with changing population density from complete independence. All too often scientists have at their disposal terms like black or white only, and nature is of varying shades of grey!

Experimental methods may be utilized to investigate ecological problems at very different levels: at the behaviour level, we may find how a plant or an animal species reacts to experimental conditions at some critical time of its life-history. Thus Tansley (1917) demonstrated that *Galium hercynicum* Weigel and *G. pumilum* Murr. would germinate equally on acid or calcareous soil, but the seedlings of the first were handicapped on calcareous soil and vice versa. Such results can be recorded quickly. At the population level we can observe how the population of a species, or an association of species reacts to changes in external conditions. Here change may be progressive over a number of years, but the result will be understood only if changes in the fertility and mortality are measured in relation to the imposed change in conditions. Both types of experiment may lead to unexpected and exciting results. Thus in the work on the winter moth near Oxford, we found that of the apparently healthy caterpillars which dropped from the oaks to the ground beneath to pupate, only 5-10 per cent produced moths in the following winter. With only small numbers present per square metre of clay soil, few could be found by digging even with a considerable effort. So experiments were set up by putting under the trees known numbers of pupae under small sheets of glass covered by sods. As expected a high proportion of pupae were soon destroyed by soil predators, but in addition many of the remaining pupae were parasitized by ichneumon flies; this was quite unexpected, and at once leads on to further experimental studies.

On the population level I think that the most striking experiment is that of N. S. Jones, who destroyed the limpets on a ten-yard strip of the beach at Port St. Mary (I.O.M.). Although limpet guts were known to contain algal fragments, the effect of their browsing on sea-weeds of the shore was unknown. In the next spring the bare rocky shore of the experimental strip became clothed with green algae, and brown algae began to establish themselves. Soon the strip was thick with *Fucus* spp. which reproduced so prodigiously that the whole shore became invaded with a dense algal growth, in which many hybrids were recorded (Burrows and Lodge, 1951). Next the limpets increased greatly and now after some 11 years conditions are once more approaching those before the experiment began. These experiments show that it is the browsing by limpets which normally keeps the rocks bare. It was quite unsuspected that the equilibrium could be upset by a change over so small an area.

The experiments which ecologists can perform in the field may either be additive or subtractive. Familiar additive experiments involve the addition of soil nutrients, water, or grazing animals. Some of the best plant ecology of this type is hidden from ecologists under the cloak of agriculture. Martin Jones (1933) in his now classic papers on the influence of nutrients and grazing on sward found that when the timing and amount of grazing were varied, either clover, cocksfoot, or rye grass predominated in the sward; he summarized the relative effects as follows: 'Although edaphic factors play their part in regard to the botanical composition and nutritive value of a pasture actually they are of only secondary importance, and quite subservient to the biotic factors, i.e. the way the management of the grazing is carried out by man.

It is possible, over a wide range of soil and climatic conditions, to control and determine the botanical composition of the sward according to the way it is grazed.' The observations can be explained in terms of plant behaviour. Each species is especially sensitive to damage at a different time, and grazing at that time suppressed its growth differentially.

Subtractive experiments have been more widely practised by ecologists, who have for instance excluded grazing animals by fences. Farrow (1917) demonstrated that heavy grazing by rabbits limited the heath flora eventually to lichens. In contrast the grazing of rough moorland by voles maintains a richer flora than when no grazing is allowed (Summerhayes, 1941). In the Kaibab Forest of Arizona the elimination of predators in the early years of this century allowed a prodigious increase in the Mule Deer, which severely affected the local flora. Then starvation reduced the numbers of deer to a tenth of their peak population (Leopold, 1943; Lack, 1954).

On a much smaller scale C. A. Fleschner of California reported to the 10th International Congress of Entomology that when he removed by hand the predatory insects from selected branches of citrus trees, the population of mites rose to very high levels.

The classic work on the bluebell by Blackman and Rutter in the *Annals of Botany* 1946-54 included a variety of experimental methods; they showed that it was the ability to withstand reduced light intensity which enabled this plant to survive in woodlands. You will find many similar examples in the stimulating presidential address to this society by Salisbury in 1929.

Curiously enough the transplant experiments performed at Potterne, which were supported by this society, and the even more extensive experiments of Clements *et al.* (1950), have provided information which has been more of taxonomic than ecological interest.

It may be argued that experimental ecology is difficult for the majority because it involves ownership of land, or at least permission from landowners. This is partly true, but plenty of big experiments have already been unwittingly set up by others, and their results can be harvested and interpreted by enterprising ecologists (see Tansley, 1939, p. 131). Soon after the First World War the Forestry Commission began planting conifers on the Brecklands of Suffolk. David Lack and his brother spent two weeks counting the birds breeding in unplanted areas and in plantations up to 11 years old (Lack, 1933). This work seems to me to be a model of careful planning, and analyses the reactions of birds to changes in a single environmental factor.

The application of methods of statistical correlation to field observations in which a number of different variables are measured can provide valuable results. Although the method is not truly experimental the analytical treatment is similar. Since variables are measured and not controlled, care must be taken that correlations which are statistically significant are not assumed to imply a causal relationship. There is danger too that time series may bedevil the statistics (Moran, 1949), and if enough correlations are tested, eventually by chance alone one will be found 'significant'. It is wise to check that there is a biological mechanism involved as well as an arithmetical one. I trust I have myself avoided these pitfalls in interpreting counts of winter moth larvae on five oaks at Wytham (Varley and Gradwell, *in press*). Each year the caterpillar population density was greatest on the same two trees, which were often seriously defoliated. These trees opened their leaves each year some days before the other three, and the biological explanation depends on the inability of newly hatched caterpillars to enter the firmly closed buds of the other trees. Lack has similarly treated as an experiment the returns of birds ringed as nestlings, and has shown the effects of clutch size on survival (see Lack, 1954).

One of the most exciting new lines in plant ecology arises from the discovery of antibiotics. Although the idea of plant interference goes back to de Candolle (1832, p. 1474) and the practice of crop rotation arose from it, the ecological implications are only now beginning to be explored. If some plants not only compete for light and nutrients, but increase their chances of survival by chemical warfare against their competitors, we must discover which plants produce these substances, and study the susceptibility of other species to their effects.

Penicillin is now a household word. It was discovered because the bacterial utilization of nutrient agar was inhibited by a diffusible substance in a zone around mould colonies. The literature on the subject is now vast, but I must refer to the paper by Thornton (1956) on the ecology of micro-organisms in soil. Thornton distinguishes three major soil environments: the colloid films on mineral grains, dead plant fragments, and lastly the surfaces of living roots, which have a population many times higher than in the rest of the soil. This is the 'rhizosphere' and its unique properties are due to the presence of nutrient exudations from the plant roots. Various sugars, amino-acids, phosphatides and other more complex substances have now been recognized. Whilst some are used by other organisms as nutrients, others have an inhibiting effect on the growth of certain species. A third type of effect is illustrated by the amino-acid asparagine, which Thorpe *et al.* (1947) found was used by wireworms in locating the roots on which they feed. Thornton stresses the many types of antagonism and competition possible between the higher plants, the bacteria, protozoa, nematodes, fungi and so on. The interactions in soil vary down to the level of plant strains: the flax variety 'Bison' is resistant to the fungus *Fusarium*, whilst 'Novelty' is susceptible to attack. Timonin showed that the roots of the two strains had an entirely different fungus flora. 'Bison' had *Trichoderma*, which antagonizes *Fusarium*. 'Novelty' lacked *Trichoderma*, but had *Cephalosporium*, *Fusarium*, *Helminthosporium* and *Verticillium*. It remains to be discovered what substance encouraging *Trichoderma* is produced by the roots of 'Bison', but the range of known root secretions is considerable (Bonner, 1950; Audus, 1953). Of special interest are substances like the unsaturated lactones coumarin and scopoletin, which are inhibitors of root growth, and also affect germination (Evenari, 1949).

The ecological significance of the presence of substances with these effects may be enormous, and this can be investigated only by experiments, both in the field and in pots, testing the ability of seeds to establish themselves in varied plant associations.

Whilst preparing this address I was delighted to find that Dr. Harper had in progress experiments of both these kinds, and he has very kindly permitted me to refer to them here. The results are sufficiently unexpected to provide considerable food for thought. The germination of the seeds of *Rumex* in the field, and in pots of soil collected from the same places, show an astonishing difference. In pots, germination was high, in all the soils tested. In the field not a cotyledon emerged! It is too early to say whether this effect is due to an evanescent chemical substance, or to the presence of some animals destroying the seeds in wild conditions. Lazenby (1955) obtained results for the establishment of *Juncus effusus* which were almost as striking.

Some ecologists have objected to the idea of experimentation on the grounds that ecological experiments take too long. Dr. Harper has also studied the effects of planting the seeds of weeds such as poppies with cereals like oats, of course keeping pure sowings as controls. He was kind enough to show me some pots six weeks after planting. Surprising results were already apparent. In the pure sowings, both poppies and cereals had produced strong plants, but in the mixed sowings, the poppies were tiny and stunted, although they had not been shaded by the slender leaves of oats. Let no one hesitate to begin experiments on the ground that they take too long!

Perhaps those plants which are weeds of cultivation are normally found only on bare soil because of a particular sensitivity to some inhibitor or inhibitors present in plant associations. Probably the strength or the nature of these inhibitors varies, and an extreme case might be found in plants like the grass *Brachypodium pinnatum* L., which often entirely dominates chalky soil, and the introduced 'Hottentot fig', *Carpobrotus edulis* L., which forms great mats on the southern coast of Cornwall, for it is obvious that no other species seem capable of germination and establishment in these conditions.

Dr. Watt, whose fine address to this society in 1947 impressed me greatly, provided an attractive theory to explain the mixed societies of heaths and grasses in terms of cyclical succession, each species providing conditions suitable for the colonization of the next. I wonder how far suitability or unsuitability is to be measured in terms of the absence of nutrients, or the presence of inhibitors? A combination of transplantation experiments, with germination experiments in the field and in the laboratory, might well give an answer.

The more I study insects and plants the more I am impressed by their interdependence. Last summer I had the privilege of representing this society at the 10th International Congress of Entomology, and afterwards I was invited to see the great area of boreal forest in New Brunswick, now exploited by the paper companies, who harvest the dominant trees, spruce and balsam fir. Over an area of perhaps 1000 square miles in this province alone the trees have recently been severely damaged or killed. Persistent defoliation by the caterpillars of the spruce budworm (*Choristoneura fumiferana* (allied to our green tortrix of oak)) was killing the trees over wide areas. Over 100 square miles a year are now sprayed from the air with insecticide to combat the pest, and in this way the trees are being kept alive. Previous severe outbreaks are known to have occurred in 1912, 1878 and about 1807; these destroyed mature trees over large areas, so that many of the surviving stands are of even age, and have grown over the fallen trunks of the stand destroyed in the last epidemic.

It is generally accepted that insect pollination has guided the evolution of floral structures of many groups of higher plants. Lipke and Fraenkel (1956) have suggested that many of the more curious chemical substances which plants produce are anti-insect, or anti-grazing adaptations. Besides spines and thorns, poison glands, oils, alkaloids, acids, tannins and a wide range of peculiar substances have probably been evolved as protective devices. The plant feeders have, of course, evolved partial or even complete immunity to some of these, and the plants have then evolved new substances, to which some herbivores have again become adapted. The insects may eventually use the chemicals as sign stimuli, or attractants by which they find the food to which they are adapted. This provides an explanation of the chemical diversity of closely allied species and strains of plants, and of the speciation process in the insects feeding on them.

I hope and believe that we are entering a new period in ecology, in which the Nature Conservancy is playing a very important role. Their responsibilities are wide, and again and again questions arise to which there is at present no answer. Solutions to their problems are being sought by extensive field experiments, over a hundred of which have been begun in a wide range of different areas. We wish them luck in their endeavours, and look forward with keen anticipation to the scientific and visible results of their experiments.

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THE FOOD OF SOME FRESHWATER CYCLOPOID COPEPODS AND ITS ECOLOGICAL SIGNIFICANCE

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(With 9 Figures in the Text)

Considering the advanced state of our knowledge of the systematics of the freshwater cyclopoid copepods and the fact that many species are abundant in natural waters it is surprising that practically nothing is known of their food and feeding mechanisms. A few casual and often contradictory statements relating to the food of the group are to be found scattered through the literature but no definite study of the subject appears to have been made. Gurney's statement (1931) that 'it is most difficult to determine the food as it is generally impossible to recognize it from the contents of the gut' is too pessimistic, for by the employment of a very simple technique the nature of the gut contents can usually be revealed.

The earliest references to the food of cyclopoids are to be found in writings dating back to the early years of the nineteenth century, but as Klugh (1927), who studied the feeding habits of certain freshwater crustaceans remarks 'the earlier writers on Entomostraca are extremely vague in their statements as to the food of these animals'. However, one of the earliest, Jurine (1820), made the observation, which seems to have been largely ignored by subsequent workers, that *Cyclops* is carnivorous. Birge (1897) (cited by Klugh 1927, and Gurney 1931) also claimed that *Cyclops* is partially carnivorous, eating rotifers, nauplii 'and other animals'. He also mentions a *Cyclops*, presumably a plankton species, feeding on *Ceratium*.

Since these early days references to the food of cyclopoids have been made by Naumann (1918), Klugh (1927) and Vetter (1927*a*, *b*), though Vetter was interested in phytoplankton and its fate rather than in the food of cyclopoids. Neither he nor Naumann made specific determinations, a fact which robs their observations of much of their value, and neither added substantially to our knowledge. Klugh's work is still the most comprehensive review of the food of the freshwater Entomostraca, though he studied only two cyclopoid copepods—*Macrocyclops fuscus* and what would now be called *Acanthocyclops bicuspidatus thomasi*. The only food which he recorded from the gut of the latter species was the alga *Chaetophora elegans*, while from the gut of *Macrocyclops fuscus* he recorded 'palmella forms', a *Chlamydomonas*, and 'chitin fragments'. However, he also observed *Macrocyclops fuscus* seizing and partially devouring small specimens of its own species and of *Diaptomus birgei*.

In addition a few casual statements from the literature deserve mention. Babák (1913), cited by Oliva & Sládacek (1950), reports an attack on the larva of an axolotl by *Cyclops* sp. and Oliva & Sládaček themselves mention cases of attacks by *Cyclops strenuus* and *C. vicinus* on axolotl larvae 2 cm in length. Similar attacks where small fishes were the victims were reported by Spandl (1926), and an account of such an incident where *Acanthocyclops viridis* was seen to attack a small fish was given by Fryer (1953), together with a mention of accounts given by aquarists of attacks on fish fry by unidentified cyclopoids. Innes (1951) also records having seen cyclopoids 'on young fishes'. Southern & Gardiner (1926) record diatoms from the gut of *Cyclops strenuus* (presumably *C. s. abyssorum*). Roy (1932) mentions the important fact that *Macrocyclops fuscus* is a willing carnivore but notes that vegetable matter is also to be seen in the gut, and concludes that it partakes of such food also; while Hintz (1951) found that *Cyclops* (species not stated) kept in captivity quickly seized and devoured mosquito larvae when these were added to dishes containing the copepods. Individual copepods consumed about five first and second stage larvae each day. Lindberg (1949) also saw *Acanthocyclops viridis* attacking mosquito larvae, and quotes Hurlbut as having seen, rather surprisingly, *Microcyclops varicans* involved in a similar incident.

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The work of Miller (1952) is also worthy of note in this connection concerning as it does the ingestion of coracidia of the cestode *Triaenophorus crassus* by *Acanthocyclops bicuspidatus thomasi*. Ruttner (1953) appears to be aware of the important fact that some planktonic cyclopoids are carnivorous for he refers to their habit of feeding on *Diaptomus*.

Although cyclopoid copepods have been cultured in the laboratory, reference to papers containing details of culture techniques gives little information on the food utilized. Horse dung infusions (essentially protozoan cultures) appear to have been the chief source of food used in cultures and Coker (1933) remarks that this medium was satisfactory for the rearing of *Acanthocyclops vernalis* and *Eucyclops agilis* (= *serrulatus*) but states that 'we had some reason to doubt its effectiveness in respect to the fertility of adults reared and as to its general suitability for *A. viridis*'. Later Coker claims to have had more satisfactory results by the addition to the culture of unicellular green algae and chopped fragments of the filamentous green alga *Mougeotia*. Klugh (1927) carried out certain culture experiments with *Macrocyclops fuscus*, the results of which were rather inconclusive, though he states that they indicate that this species is omnivorous. A critical examination of his results in the light of experience gained during the present study, however, indicates that when his specimens which had been supplied with algae died they did so because of starvation, and that those which survived did so either because of the short duration of the experiment or because of the development in the cultures, admitted by Klugh, of protozoans which were utilized as food. Lowndes (1928) also used protozoan cultures as food for cyclopoids but observed that *Acanthocyclops vernalis* shows a tendency towards canibalism.

MATERIAL AND METHODS

The species studied have been mostly common ones belonging to several different genera which are, however, sufficiently closely allied to be regarded as subgenera by some, and include species with widely differing ecological preferences. The work consisted mainly of an examination of the gut contents and to a lesser extent of experiments. Gut analyses were made on living animals, usually shortly after collection in the field. The technique employed is very simple and consists merely of placing a single specimen in a drop of clean water on the surface of an old-fashioned 'live box' and covering it with a circular cover slip whose diameter exceeds that of the window in the box. The raised nature of the 'live box' enables fingers to be employed in the manipulation of the cover slip, and by this means one can with a little practice manœuvre the copepod into the desired position. For gut analyses the best position is that in which the copepod lies on its side. Once in this position careful pressure exerted on the cover slip causes the gut contents to be exuded, usually through the ruptured cephalothorax. On most occasions it is possible to keep separate the contents of the stomach and rectum. Special attention may be drawn to the fact that when the gut contents are extruded as a compact mass it is frequently impossible to distinguish the individual constituents until further pressure is exerted and the contents are smeared across the field of vision. It seems probable that some of the vague reports of cyclopoid guts containing 'greenish mush', etc., are the result of insufficient maceration of the often compact contents.

THE FOOD OF INDIVIDUAL SPECIES

In the following section an attempt is made to summarize the results of gut analyses made on a large number of specimens of various species discussed in turn.

Macrocyclops albidus (Jurine). The gut contents of 136 specimens, mostly adult females but including some adult males and a few stage V copepodid stages were examined. The material was obtained from eleven different bodies of water embracing several different habitats, mostly in the English Lake District. In addition one specimen of the African 'subspecies' *M.a. oligolasius* has been examined. The results of these analyses are illustrated in Fig. 1. The food taken consists largely of animal matter, more than 73% of the guts containing such material. Plant material (essentially algae) was found in just over a quarter of the guts examined but it is certain that most of it was derived from the guts of herbivorous animals which had been ingested. Indeed, on several occasions the plant material recorded could definitely be seen to be confined within the gut of an organism which was itself contained within the gut of the copepod, and in several cases the records of algae concern only a single minute diatom or other algal fragment which, while comprising a negligible percentage of the gut contents of an individual specimen are nevertheless recorded in the figures. The fact that even starving individuals will not partake of certain algal foods when these are supplied, though they feed readily on animals similarly supplied, is further strong evidence that algae are not as a general rule eaten by this species. After feeding on an herbivorous animal the gut frequently gives the impression that the copepod itself had eaten algae.

When the detailed composition of the food is considered it is seen that other copepods, both cyclopoid and calanoid, comprise a considerable proportion of the prey. When identification was possible the former were often found to belong to smaller species such as *Eucyclops agilis* and probably other members of this genus. These are later shown to be herbivorous species. In addition cyclopoid egg sacs, without the copepod which once bore them, have been definitely identified in the gut on several occasions. It seems probable that these structures owe their presence in the gut to the fact that the predacious copepod attempted to seize an egg-sac-bearing copepod but succeeded in grasping instead an egg sac which parted from its carrier and was then ingested. The feat of swallowing these delicately constructed egg sacs without causing more than very slight damage, has interesting implications which are discussed in a paper on the feeding mechanism. The presence of the remains of oligochaetes in 11% of the guts and dipterous larvae in more than 7% is especially interesting for often these organisms are considerably larger than the copepod preying on them.

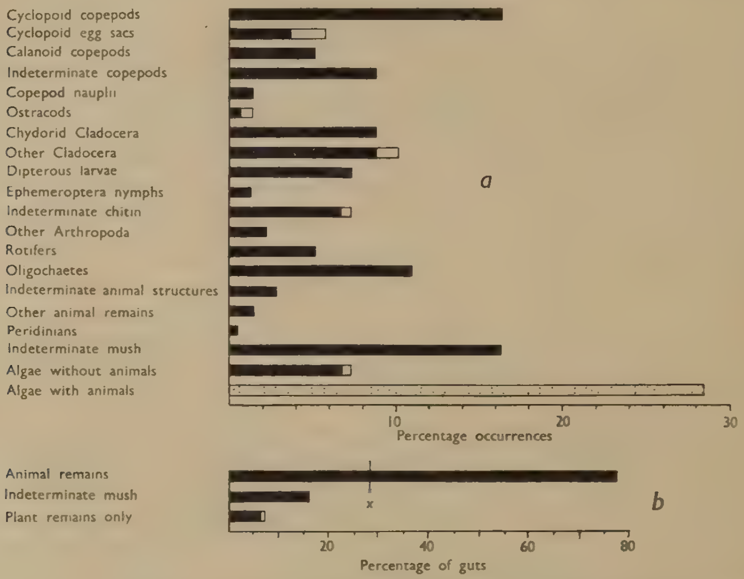

Fig. 1. The food of *Macrocylops albidus*: *a*, detailed; *b*, general composition.

The line at X indicates the percentage of guts with animal remains which also contained plant remains, many of them certainly derived from the guts of ingested organisms. Blank columns indicate determinations subject to doubt. Stippling indicates food probably derived from the guts of prey.

About 16% of the specimens examined contained only unidentifiable 'mush' whose colour varied from grey to a rich brown; the latter being the colour often associated with animal remains. Judging from the predominantly carnivorous diet of this species it is suggested that this mush, or much of it, is derived from softbodied organisms such as small triclad and rhabdocoele turbellarians and large protozoans which frequently occur in the same habitats as *M. albidus* and which must often be encountered whilst the latter is foraging for food. Such organisms quickly disintegrate and would leave no structural remains in the gut.

The amount of material which can be stored in the gut is remarkable, and remains of several organisms are often found in a single gut. Thus a specimen obtained from Blelham Tarn on 28 October 1952 contained, as shown by the presence of post-abdomens, no fewer than four specimens of the cladoceran *Ceriodaphnia pulchella*, three in the stomach and one in the rectum. That not only the post-abdomen was eaten was shown by the presence of numerous foliaceous appendages, mandibles, etc. It is no uncommon thing to find the remains of two or three cladocerans or copepods in a single gut, perhaps also accompanied by other remains.

The most remarkable gut contents of this, or any other species, that were seen were those of an adult female taken from Esthwaite Water on 14 November 1952. Its stomach contained the remains of copepodid stages of two cyclopoid copepods which had been engulfed whole and which, while damaged, were entire within the gut (these measured about 360 μ and 530 μ in total length respectively); the remains of a third cyclopoid copepod which also had probably been swallowed whole as the furcal rami and a large part of the body were present; the remains of a fourth cyclopoid copepod, in this case somewhat mangled; the remains of a chydorid cladoceran which had also apparently been engulfed in its entirety for an antenna, numerous thoracic appendages, and the coiled gut were present; nine oligochaete chaetae; and the skeleton of a single diatom. Had this not actually been seen it would have been difficult to believe that so much material could be forced into a single stomach. Unfortunately this specimen, a robust individual, was not measured, but it may be noted that the maximum length attained by this species does not exceed 2·5 mm.

In addition to the evidence obtained from gut analyses that this is a markedly carnivorous species, a number of feeding experiments prove conclusively that *M. albidus* is an exceedingly voracious species, which attacks, kills and devours organisms much larger than itself. Thus on numerous occasions specimens kept in captivity and supplied with dipterous larvae or with oligochaetes have been observed to kill and eat them.

That a very small amount of vegetable matter may be ingested by *M. albidus* but that this is an unusual occurrence, was shown by an experiment in which a number of specimens were starved for some time and then supplied with a mixed culture of *Micractinium* sp. and *Scenedesmus* sp. While, even after three days in the presence of the algae, the guts of the majority of the specimens remained empty, traces of the algae supplied were found in a few guts through which, incidentally, it passed undigested. A possible explanation why such algae were occasionally ingested in this manner may be that a number became agglutinated to form a seizable object to the hungry copepod which, under the circumstances, swallowed anything it could grasp. Filamentous green algae, which constitute an important part of the diet of several herbivorous species, remained untouched by starving specimens of *M. albidus* when the latter were confined with it.

Macrocyclops fuscus (Jurine). The gut contents of forty-four specimens, mostly adult females, obtained from eight different bodies of water, mostly in the English Lake District were examined. The result of these gut analyses are shown in Fig. 2. Like the closely related *M. albidus*, *M. fuscus* is essentially a carnivorous species. The gut contents were less diverse in nature than was the case in *M. albidus*, but this can probably be attributed to the fact that a considerably smaller number of specimens was examined. The remarks concerning the presence of vegetable matter in the guts of *M. albidus* apply equally to *M. fuscus*, for it seems that the major portion of such material which is found in the guts is derived from the guts of organisms which have themselves been taken in as food. Likewise, the remarks on the probable origin of the structureless mush made when *M. albidus* was discussed also apply here.

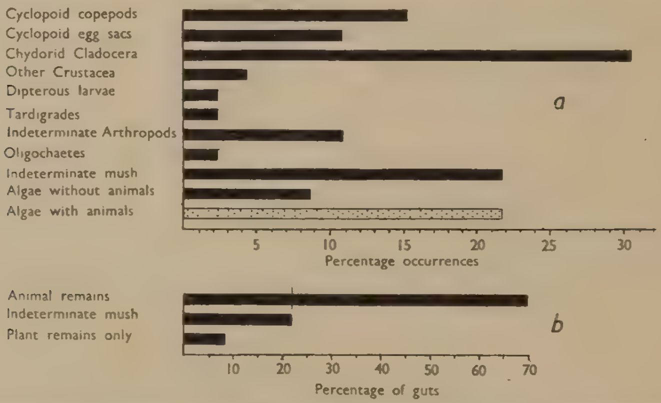

Fig. 2. The food of *Macrocyclops fuscus*: *a*, detailed; *b*, general composition. Conventions as in Fig. 1.

Acanthocyclops viridis (Jurine) (Placed in the genus *Megacyclops* by some systematists.) The gut contents of fifty-one specimens, mostly adult females, obtained from eleven different bodies of water, mostly in the English Lake District, were examined. The results are shown in Fig. 3. Like *Macrocyclops albidus* and *M. fuscus*, this species feeds largely on animal material, a fact which has been verified by feeding experiments. In general the items figuring in the diet are more or less the same as the two species previously considered but the proportions differ. The analyses indicate a higher frequency of oligochaetes (21.6% of the guts) and dipterous larvae (15.7%) in the guts than was noticed for either *M. albidus* or *M. fuscus*, and a smaller proportion of cladoceran remains. It is of interest that while cladoceran remains occurred in approximately 6% of the guts none of these records refer to chydorids, though these organisms figure largely in the diet of

M. albidus and would appear to be a very important source of food for *M. fuscus*. The ecological importance of these dietary differences in carnivorous species is discussed in a subsequent section of this paper.

While most of the algal material seen in the alimentary canal was derived from the guts of animals eaten by the copepod, there is some evidence that one type of alga was deliberately taken in. This was a colonial form of the *Schizochlamys* type whose cells are embedded in a gelatinous matrix. It occurred in four of the six guts whose recognizable contents consisted solely of plant material and was also seen twice in guts in which animal remains occurred. These algal colonies form distinct solid masses of a consistency which is probably not unlike that of certain small animals, and it is suggested that a browsing copepod encountering such a body receives sensory stimuli similar to those received when animal matter is encountered and responds accordingly. All such algae pass through the alimentary canal quite unharmed.

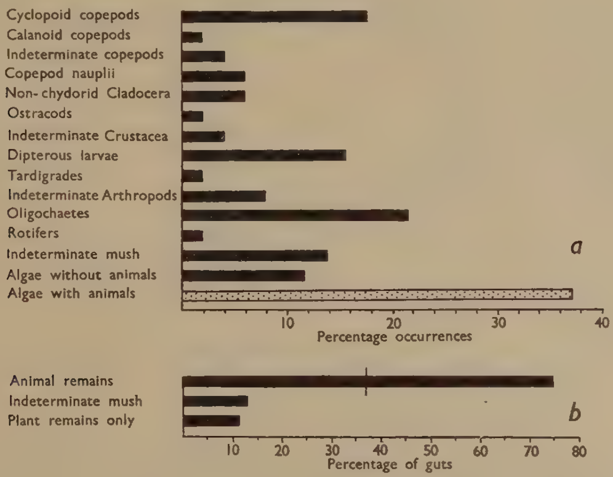

Fig. 3. The food of *Acanthocyclops viridis*: *a*, detailed; *b*, general composition. Conventions as in Fig. 1.

Cyclops strenuus abyssorum Sars. The gut contents of 107 specimens, mostly adult females, were examined. The majority of them were obtained from plankton samples taken in both the north and south basins of Windermere, but gut analyses were also made on seven specimens from Coniston Water and on twenty-four specimens from Loch Lomond. This species, being planktonic, lives under quite different conditions to those previously considered, which are all essentially littoral and pond-dwelling forms. The results of the gut analyses are shown in Fig. 4. The figures show that animal material is the most important element in the diet of *C. strenuus abyssorum* and that, of the organisms preyed upon, the calanoid copepod *Diaptomus* is by far the most important, at least in the three lakes from which specimens were obtained.

Considering the abundance of other organisms (*Daphnia*, *Bosmina* and rotifers) in the plankton samples from which the specimens were obtained, and the relative infrequency with which they occurred in the guts in comparison with *Diaptomus*, one is justified in concluding that *C. s. abyssorum* shows a definite preference for the latter, a factor which is of some importance so far as the dynamics of plankton populations are concerned.

Although most of the algal remains recorded from the guts of the specimens examined were probably derived from the alimentary canals of *Diaptomus* with whose contents (see Fryer 1954) they showed a marked similarity, there is evidence that this species does take in a limited amount of such food directly. Thus slightly more than 10% of the specimens contained algal remains unaccompanied by animals from which they could have been derived, and some of these algae (occasional colonies of blue-green algae and large desmids) were unlike those which were utilized as food by the other constituents of the zooplankton (*Diaptomus*, Cladocera and Rotifera) which comprised the animal food of this species. In most cases the algae which were presumed to have been ingested directly were of relatively large size.

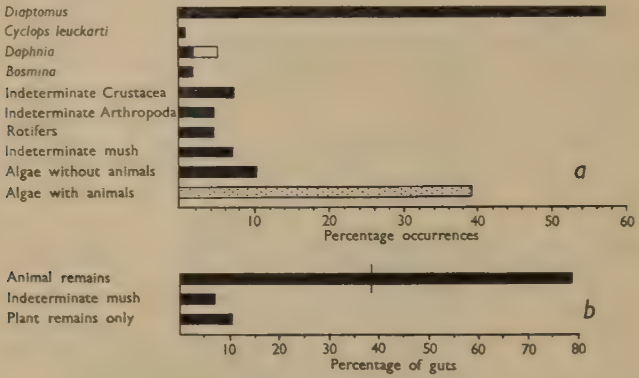

Fig. 4. The food of *Cyclops strenuus abyssorum*: *a*, detailed; *b*, general composition. Conventions as in Fig. 1.

Cyclops strenuus s.str. Fischer. This species has not been studied in detail but it may be placed on record that crustacean remains have been seen in the gut of specimens obtained in Yorkshire.

Eucyclops agilis (Koch, Sars). The gut contents of 106 specimens, mostly adult females, were examined. These were obtained from thirteen different bodies of water mostly in the English Lake District. The habitats ranged from the littoral zone of lakes to small springs. The results of these analyses are shown in Fig. 5. The diagrams indicate that, unlike those species previously considered, *E. agilis* is essentially a vegetarian, feeding on a wide variety of algal foods. The most important of these appear to be diatoms and filamentous green algae which occurred respectively in 67% and 49% of the guts examined. Colonial and unicellular green and blue-green algae (between which it is often impossible to differentiate when the former are broken up in the stomach) are also of importance, for between them they were recorded from 50% of the guts.

The size of the diatoms eaten varies tremendously, both very large and very small specimens being swallowed. Some of the naviculoid types are so large as to cause one to marvel how they can be ingested and how, when once swallowed, they fail to pierce the gut walls; while the presence in the alimentary canal of the very small forms causes equal perplexity when the available food collecting mechanism is considered. It should be emphasized that in the case of this and other algal-feeding cyclopoids, diatoms are swallowed whole and are not pounded and broken by the mandibles as might be suspected from an examination of these heavily chitinized structures. It is rare to find a broken diatom in the gut. In this respect they differ markedly from marine planktonic copepods (mainly calanoids) which, according to Lebour (1922) 'certainly crush the hard shells, such as the diatom cells, very few of which come through [the gut] whole except very small valves such as *Thalassiosira*'. A wide range of diatom species is eaten. The exact identification of these is a matter for an expert on the group, but it can be stated that those of the naviculoid type (*Navicula*, *Nitzchia*, etc.) predominated, while other genera such as *Amphora*, *Tabellaria*, *Cymbella*, *Melosira*, *Gomphonema*, *Gyrosigma* and *Asterionella* were recognized in that order of frequency.

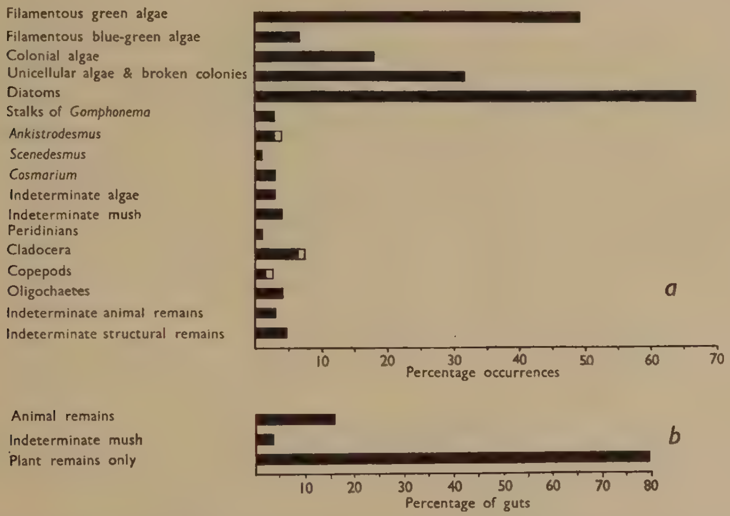

Fig. 5. The food of *Eucyclops agilis*: *a*, detailed; *b*, general composition. In (*b*) for direct comparison with carnivorous species only guts containing plant remains *only* are shown in the lowest column. The actual percentage of guts containing deliberately ingested plant material is therefore probably even higher than is indicated.

Perhaps the most striking fact concerning the food of this species is the discovery that filamentous algae are utilized to a large extent. Considerable amounts of this material are often present in the stomach which is sometimes crammed with long filaments compounded into a compact mass. Quite long filaments are swallowed, some as long as 340 μ having been recorded. This length is quite considerable when one takes into account the fact that the largest specimens of *Eucyclops agilis* have a total length of only about 1·4 mm and a stomach only about one-third of this length.

The wide range of algal types eaten helps to explain the equally wide range of environmental conditions in which this species is found, for such food as it appears to require is seldom lacking in any body of freshwater capable of supporting life. Availability rather than deliberate selection seems to govern the type of algae eaten. Thus specimens collected from the muddy bottom of a tarn devoid of macro-vegetation were feeding on diatoms, which appeared to be the only green plants present, while on the other hand specimens taken from a water-filled trough, on the walls of which filamentous algae grew to the apparent exclusion of other algal types, were feeding on this material. Similarly specimens dwelling among reeds, on whose stems were encrusting growths of diatoms such as *Tabellaria* and *Gomphonema*, were feeding on these species, and specimens frequenting the surfaces of submerged stones were browsing on the mixed 'Aufwuchs' associated with the latter.

The fact that *Melosira* and *Asterionella* were recorded from ten and two guts respectively should not be interpreted as indicating that this species feeds on the plankton as such, for these two planktonic diatoms were definitely taken up from the bottom where they had settled and where *Melosira* at least passes part of its life cycle (Lund 1954).

Animal remains were found in only a few of the guts and these remains were usually very fragmentary. For example, of the four cases in which oligochaetes were recorded one concerned the occurrence of a single chaeta and another of two such structures. The same applies to some of the cladoceran remains, two cases concerning only the post-abdominal claws of these organisms. It is not claimed that animal matter is not deliberately taken on occasion, as it probably is, but the evidence points to the fact that it is taken only rarely and then rather by chance encounter than as a result of deliberate seeking.

Eucyclops macruroides (Lilljeborg). The gut contents of 112 specimens, mostly adult females, taken from seven different bodies of water, mostly in the English Lake District, were examined. The results of these analyses are shown in Fig. 6. The diagrams reveal that the composition of the diet is remarkably similar to that of the closely allied *E. agilis*, but in this species the proclivity towards a carnivorous diet is even less marked than in *E. agilis*, for animal remains, on the whole very fragmentary, were recorded from only 8% of the guts studied. There can, however, be no doubt that *E. macruroides* does occasionally deliberately ingest small animals, for a specimen kept in captivity was observed to swallow a living rotifer. Nevertheless, the diet consists essentially of algae and it is as an algal feeder that *E. macruroides* must be considered in ecological studies.

The comments made concerning the diversity of algal foods eaten by *E. agilis* and the remarks appertaining to the ingestion of diatoms and long filaments of algae apply equally well in the case of *E. macruroides*. The maximum length of this species is only about 1.2 mm, yet the longest algal filament seen in a stomach had a length of 380 μ.

Eucyclops macrurus (Sars). The gut contents of thirty-two specimens, mostly adult females, taken from three bodies of water in the English Lake District, were examined; the results are shown in Fig. 7. Although the data concern only a relatively small number of individuals, the results suffice to show that the food preferences of this species are very similar to those of the closely allied species *E. agilis* and *E. macruroides*. If the surmises concerning the origin of unidentified mush made earlier are correct then its presence in eight (25%) of the guts examined may indicate that protozoans and other small and easily disintegrated forms are eaten to a considerable extent, but the available information is too scanty and the number of individuals examined is too small to permit the drawing of any conclusions in this respect, and for the present we must be content to designate *E. macrurus* as essentially an algal feeder eating largely the same kinds of food as *E. agilis* and *E. macruroides*.

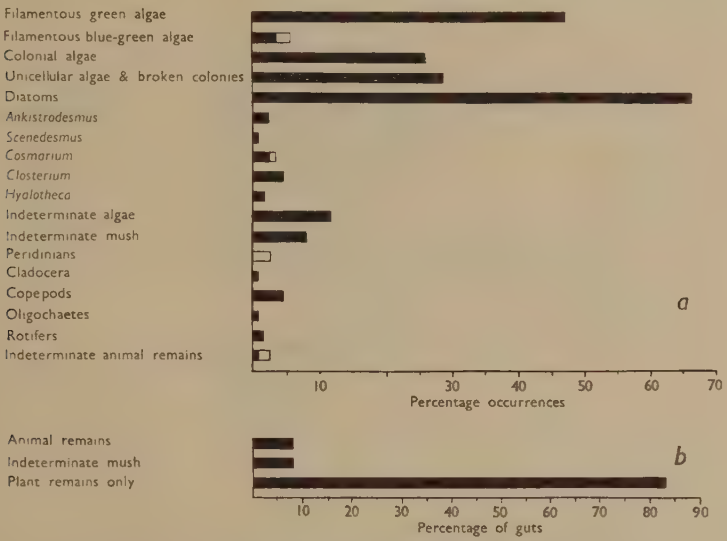

Fig. 6. The food of *Eucyclops macruroides*: *a*, detailed; *b*, general composition. Conventions as in Fig. 5.

Eucyclops gibsoni (Brady). In contrast to the majority of species examined, which occur commonly in Britain, this is essentially an African species of wide distribution in that continent. Twelve specimens were examined from one locality in Nyasaland and their food was found to consist mainly of filamentous green algae, though a number of rotifers, which abounded in the rather restricted habitat from which the specimens were obtained, were also seen in the guts. From this somewhat scanty evidence, therefore, it would appear that, like the three members of the genus studied in Europe, *E. gibsoni* is an algal feeder which will also take a little animal matter if it is available.

Eucyclops dubius (Sars). An examination has been made of the food contained in the guts of a few specimens of this species obtained from Lake Nyasa, to which lake it is believed to be confined. In all cases it was of vegetable origin, diatoms predominating. It thus appears to have similar food preferences to the other species of *Eucyclops* which have been studied.

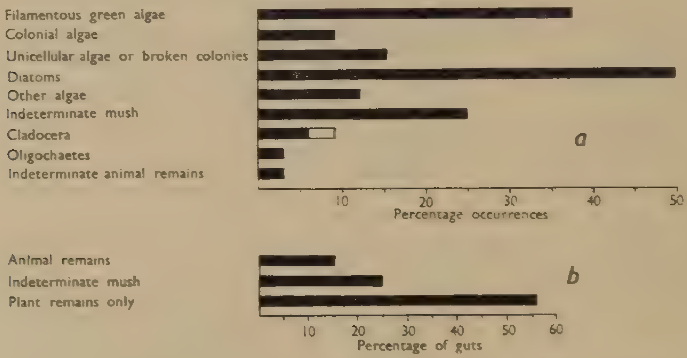

Fig. 7. The food of *Eucyclops macrurus*: *a*, detailed; *b*, general composition. Conventions as in Fig. 5.

Mesocyclops leuckarti (Claus). The gut contents of fifty-five specimens were examined, thirty of these being taken from the plankton of Loch Lomond (Scotland) and the rest being collected from the plankton of Lake Nyasa. The results of these analyses are shown in Fig. 8. The diagrams indicate that the two planktonic populations of *M. leuckarti* studied feed predominately on animal food, eating the other crustaceans and rotifers of the plankton, but there is some evidence that occasional large diatoms may be deliberately ingested.

Acanthocyclops vernalis (Fischer). The gut contents of fifteen specimens from the English Lake District have been examined and these indicate that this is a markedly carnivorous species, for the remains of oligochaetes were found in five specimens, and remains of cyclopoid copepods, their egg sacs, chydorid cladocerans and rotifers have also been seen.

Acanthocyclops venustus (Norman & Scott). Only a very few specimens, collected near Huddersfield, Yorkshire, have been studied from the point of view of feeding habits. Rotifers and copepod nauplii have been recorded as food, indicating at least carnivorous tendencies. Algal fragments have also been noticed in the gut, but an insufficient number of specimens has been studied to decide whether these were deliberately ingested or were derived from the gut of the prey. Judging from the restricted size of some of the habitats in which this species occurs, however (Fryer 1953, 1955), where animal prey—save its own nauplii—must be very scarce, one might expect it to include algae in its diet.

Acanthocyclops bisetosus (Rehberg). (Placed in the genus *Diacyclops* by some systematists.) The gut contents of several specimens of this species collected in various parts of west Yorkshire have been examined. In some cases the alimentary canal was filled with small spherical algae which may have represented macerated colonies, while diatoms, *Scenedesmus* and small colonial algae have also been recorded. These show that this is undoubtedly a herbivorous species.

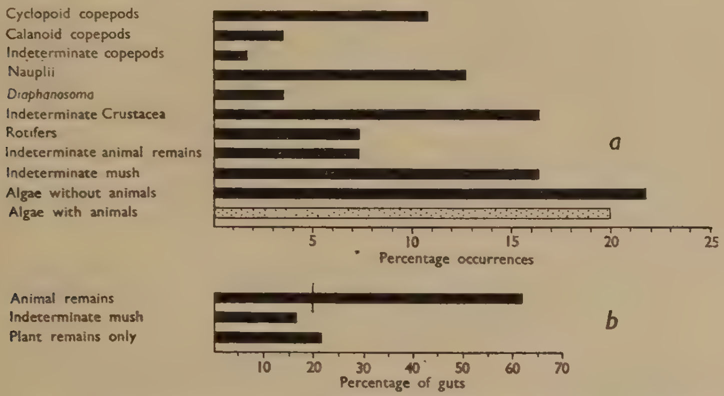

Fig. 8. The food of *Mesocyclops leuckarti*: *a*, detailed; *b*, general composition. Conventions as in Fig. 1.

Acanthocyclops languidus (Sars) (also called *Diacyclops languidus*). On several occasions the guts of specimens of this species collected in west Yorkshire have been observed to contain masses of algal material and it appears to be an undoubted herbivore.

Ectocyclops phaleratus medius Kiefer. No gut analyses have been carried out on this species, but whilst examining a living adult female in Central Africa it was observed to seize and devour an unidentified copepodid stage of a cyclopoid.

Microcyclops spp. Observations on several species of this group collected in Nyasaland, some of which have recently been described as new, have indicated that they are essentially algal feeders. One species, *M. nyasae* Fryer, which is common in certain habitats in Lake Nyasa and which feeds largely on small algae attached to submerged vegetation, also, however, has been found to include small rotifers in its diet. Taking the genus *Microcyclops* in its widest sense to include *Metacyclops*, etc., it includes several species, all of small size, which have been found to inhabit the interstitial spaces of sandy beaches in Lake Nyasa. These species, some of which are described elsewhere (Fryer 1956) appear to feed on vegetable matter which collects between the sand grains amongst which they live. Their small size (they are often less than 0·5 mm in length) and the consequent minute size of their mouth parts will enable them to seize and feed upon very small particles, but there is nothing to suggest that the feeding mechanism is in any way different from that of their larger relatives which have been studied in detail.

THE INABILITY OF CYCLOPOIDS TO DIGEST CERTAIN ALGAE

Before the present study was begun interest in the inability of cyclopoids to digest certain algae was aroused by the finding of apparently undamaged specimens of *Scenedesmus* in the rectum of *Acanthocyclops bisetosus*. During the course of the present work this phenomenon was repeatedly encountered, and it can be definitely stated that almost any small green or blue-green alga such as *Scenedesmus* or *Cosmarium* which is swallowed without having its walls ruptured, is almost certain to emerge from the anus undamaged. This applies also to any alga, green or blue-green, colonial or solitary, which is invested with a gelatinous sheath, e.g. *Tetraspora* and its allies among the green algae and *Merismopedia* among the blue-green algae. On the other hand, diatoms, while seldom or never broken up when eaten, seem almost invariably to be completely digested. This phenomenon has been noticed in both Crustacea (Vetter 1937*a*, *b*, Harvey 1955, p. 113) and fishes (Velasquez 1939, Fish 1950). As Fish remarks, the reason for this difference in digestibility would appear to lie in the different nature of the cell walls of diatoms and other algae. Velasquez makes the interesting suggestion that vegetarian fishes may selectively influence algal populations in the body of water in which they occur as they return certain groups to the water alive and these may take the place of the more valuable food algae which are digested, and notes that this may be of importance in fish-pond practice. Here it only needs to be pointed out that if fishes are important in this respect then freshwater copepods, because of their high numerical density, must often be even more important, and one can visualize conditions under which their presence could be highly detrimental to herbivorous fishes.

While the inability of cyclopoids to digest cells whose walls remain unbroken may be readily explained by the absence of any cellulase enzyme, it is less easy to explain the fact that in certain experiments herbivorous cyclopoids readily ingested expressed chloroplasts of *Spirogyra* but failed to digest them (Fryer 1957). It seems that there must either be a fundamental difference in the chemical nature of the chloroplasts of certain filamentous algae and those of diatoms (which are very readily digested); or that a certain amount of the chloroplast of the former may be digested but that sometimes its bulk is too great to permit digestion of the whole, and that the undigested material present in the rectum represents an excess over requirements. So far as the second possibility is concerned casual observations indicate that such a state of affairs may prevail in certain terrestrial gastropod molluscs when supplied with a superabundance of food, for their faeces are often distinctly green under such conditions. A third possibility is that even after rupture of the cell walls the chloroplast is not exposed to the action of digestive juices but is protected by a layer of non-digestible material. These problems are outside the scope of the present article but they are nevertheless worthy of bringing to notice for they involve some fundamental aspects of nutrition among natural populations. It may be remarked in conclusion that not all filamentous green algae are resistant to the digestive processes of herbivorous cyclopoids, for often large amounts of such algae whose contents have been completely digested are to be found in the rectum.

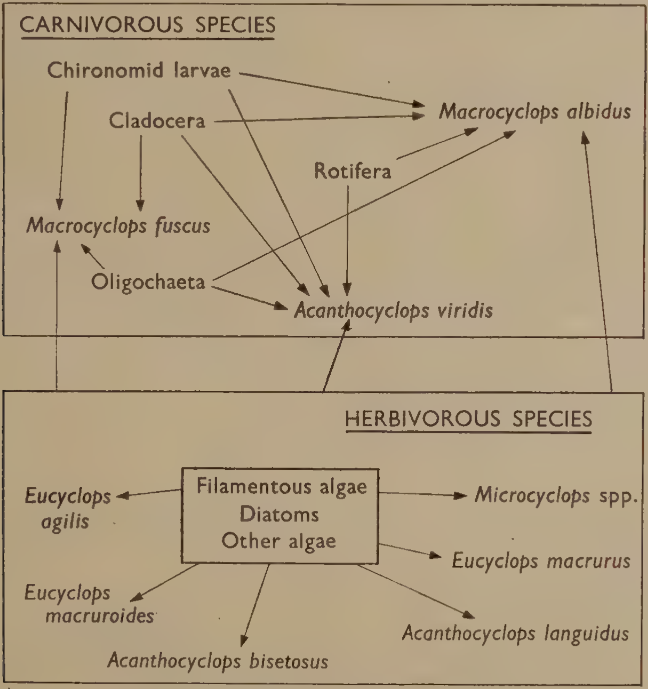
CARNIVOROUS SPECIES
Chironomid larvae
Cladocera
Macrocyclops albidus
Rotifera
Macrocyclops fuscus
Oligochaeta
Acanthocyclops viridis
HERBIVOROUS SPECIES
Filamentous algae
Diatoms
Other algae
Eucyclops agilis
Microcyclops spp.
Eucyclops macrurus
Eucyclops macruroides
Acanthocyclops languidus
Acanthocyclops bisetosus

Fig. 9. Simplified scheme of the trophic interrelationships of the commoner littoral and pond-dwelling copepods.

ECOLOGICAL IMPLICATIONS OF CYCLOPOID FOOD PREFERENCES

The part played by cyclopoid copepods in the energy flow within freshwater habitats can now be considered in the light of the knowledge gained during the present work. Fig. 9 represents schematically the main feeding relationships of the commoner European species found in ponds and in the littoral region of lakes. Certain species common in some districts are, it is true, omitted (e.g. *Cyclops* *strenuus*), but such investigations as have been made indicate that most, if not all, of these species will fall readily into one or other of the two groups here portrayed. The inclusion of '*Microcyclops* spp.' among the herbivores is based on evidence obtained from African species of this genus, of which one at least (*M. varicans*) occurs in Europe.

When the terminal links of food chains among the littoral communities are considered it is revealed that the carnivorous species fulfil an hitherto unsuspected role, for, by eating organisms such as dipterous larvae and oligochaetes they enter into direct competition with fish which take the same sort of food, but which, in some cases, do not feed to any extent on the copepods concerned. The fact that, on the whole, the carnivorous cyclopoids probably eat younger and smaller stages of these organisms than do fish, does not materially alter the argument. The important feature of the carnivorous species so far as competition with fish is concerned, is that they often occur in enormous numbers in the littoral region of lakes and smaller bodies of water. Numerical data on the abundance of these organisms are very scarce in the literature, but Smyly (1952) gives some figures from which it is possible to calculate that in a not particularly productive tarn in the English Lake District there were present throughout the year among the marginal weeds an average of some 104 *Acanthocyclops viridis* and 65 *Macrocyclops albidus* per square metre of bottom at each of five stations sampled. It is probably safe to say that the total population of these two cyclopoids consumes annually a greater number of chironomid larvae than do the fish of the tarn. Smyly's figures, incidentally, reveal also that the two herbivores *Eucyclops agilis* and *E. macruroides* which also occur in the tarn in considerable numbers are less abundant among the weeds than are the carnivores.

From the point of view of pisciculture therefore, the presence of carnivorous cyclopoids is to be regarded as undesirable, partly because they eat food which would otherwise become available to fish, and partly because of the danger to which newly hatched fry are subjected by exposure to the attacks of these predatory crustaceans. On the other hand, it would appear that the presence of benthic herbivorous species is often highly desirable, for they are important as converters of plant material into animal protein, and apart from any nutritive value which they may in themselves possess they play a part in regulating the development of littoral algae. It is unfortunate that reports on the stomach contents of fish usually refer to '*Cyclops*' and give no indication of the species involved, and indeed writers frequently fail to discriminate convincingly between littoral and planktonic species. Because of this it is impossible to decide whether herbivorous species are eaten more than are the carnivores or vice versa. Such data would be of considerable biological and possibly economic interest.

The work on the two planktonic species studied—*Cyclops strenuus abyssorum* and *Mesocyclops leuckarti*—helps to throw some light on the part played by cyclopoids in the food cycles of the freshwater plankton. The role of *C.s. abyssorum* is quite clear. In the lakes in which it has been studied it is an active predator feeding chiefly on the calanoid copepod *Diaptomus*. As some species of the latter almost always accompanies the cyclopoid concerned it can be assumed that *Diaptomus* usually forms an important part of the diet of *C.s. abyssorum*, but when no species of *Diaptomus* is present it seems probable that Cladocera and rotifers, both of which have been recorded as food even when *Diaptomus* is available, will form the main food of this species, but actual gut analyses of this species from such a lake are very desirable.

Close generic affinity in all cases studied is paralleled by similarities in the food taken, so it seems permissible to predict that the species and subspecies which are very closely related to *C.s. abyssorum* and which replace it in many European lakes (e.g. *C. lacustris, C. vicinus*) will prove to be carnivores fulfilling a similar role to their relatives.

Data concerning the food of planktonic races of *Mesocyclops leuckarti* have been obtained from only two sources, but they indicate that this is, to some extent at least, a predatory species, and that calanoid copepods, cladocerans and rotifers figure in its diet.

SIZE AND FEEDING HABITS

Since the possibility that size differences in closely allied species may be correlated with differences in food and feeding habits was first pointed out by Huxley (1942, pp. 280-1), considerable attention has been paid to this matter, particularly among birds and mammals. All the species of cyclopoids which have been studied are fairly closely related, so much so that a good case can be made out for regarding the various genera discussed as subgenera of a single genus (Gurney 1933). In general it can be said that large species tend to be carnivorous (e.g. *Macrocyclops albidus*, *M. fuscus* and *Acanthocyclops viridis*), while the smaller species tend to be herbivorous (e.g. *Eucyclops* spp. and *Microcyclops* spp.). Competition for food between a large species and a small species, ignoring for the moment the complications arising when the latter forms part of the prey of the former, is therefore negligible.

Among the herbivores there is no doubt that the very small species, e.g. those belonging to *Microcyclops* and allied genera, take smaller algal particles than do the somewhat larger herbivorous species such as the four species of *Eucyclops* studied. A relatively large herbivore can therefore co-exist in the same general habitat as a small herbivore and not compete to any significant extent for food.

It so happens that each of the two groups of very closely allied species most intensively studied contains species which are more or less similar in size. These raise problems which are quite different from those briefly mentioned here and are discussed in the following section.

COMPETITION FOR FOOD AMONG RELATED SPECIES

In general, the freshwater cyclopoids examined are either markedly carnivorous or are confirmed herbivores, and closely related species have similar food preferences. These findings are worthy of more detailed analysis from the point of view of food preferences and competition for food among closely allied species living in the same habitat. The problems are best considered by reference to specific examples.

Among the carnivores similarity of the gut contents of species living in the same habitat and employing the same type of feeding mechanism indicates that some competition for food may be expected. Table 1 shows the percentage occurrences of the main food material found in the guts of the two very closely allied species *Macrocyclops albidus* and *M. fuscus* and also, for comparison, *Acanthocyclops viridis* which although placed in a different genus is nevertheless closely related to these two species, is very similar in structure, employs a similar feeding mechanism, and exhibits similar ecological preferences. While all the animals were not collected together the collections were sufficiently random to permit comparison in this way. Unfortunately the data for *Macrocyclops fuscus* are based on the examination of the contents of only forty-four guts, but, bearing this limitation in mind, a few reliable facts can still be deduced from the table.

Table 1. *Comparison of the percentage occurrences of the main foodstuffs of three carnivorous cyclopoids:* Macrocyclops albidus, M. fuscus *and* Acanthocyclops viridis

	Percentage occurrences		
	Macrocyclops albidus	*M. fuscus*	*Acanthocyclops viridis*
Cyclopoid copepods	16·2	15·2	17·7
Egg sacs of cyclopoids	3·7+2·2?	8·7	–
Calanoid and indeterminate copepods	18·0	–	5·9
Nauplii	1·5	–	5·9
Chydorid cladocerans	8·8	30·4	–
Other cladocerans	8·8+1·5?	–	5·9
Dipterous larvae	7·4	2·2	15·7
Other arthropods	12·5	17·4	15·7
Oligochaetes	11·0	2·2	21·6
Rotifers	5·2	–	2·0
'Mush'	16·2	21·9	13·7
Algae (freely ingested?)	7·3	8·7	11·8

It can be seen that whereas all three species feed with approximately equal frequency on some foods such as other cyclopoids, they appear to show definite preferences in other respects. Thus *Acanthocyclops viridis* seemed to show a very distinct preference for large organisms such as dipterous larvae and oligochaetes. Dipterous larvae occurred about twice as frequently in this species as in *Macrocyclops albidus* and about seven times as frequently as in *M. fuscus*. Again *M. fuscus*, while apparently not taking non-chydorid cladocerans, which were eaten to some extent by both *M. albidus* and *Acanthocyclops viridis*, seems to have a distinct preference for chydorid cladocerans. More than 30% of the guts examined contained these crustaceans, whereas only 8·8% of those of *Macrocyclops albidus* contained them and they did not appear to have been eaten at all by *Acanthocyclops viridis*.

These species quite frequently co-exist in nature. All three were found together on two occasions in Wise Een Tarn in the English Lake District during the present investigation, and it is interesting to note that they tended to be feeding on different foods. Only two specimens of *Macrocyclops fuscus* were collected here and both had eaten chydorid cladocerans, an item which did not figure in the diet of the more numerous specimens of *Acanthocyclops viridis* and which was of small importance in the case of *Macrocyclops albidus*. Half of the specimens of *Acanthocyclops viridis* had eaten dipterous larvae but none had been taken by the other two species, and 60% of the specimens of *Macrocyclops albidus* had taken cyclopoid copepods as opposed to about 33% in the case of *Acanthocyclops viridis*. It would appear, therefore, that although a considerable overlap of food preferences occurs among the carnivorous species studied, there is sufficient differentiation to obviate any serious detrimental effects from competition for food.

Turning to the herbivores a rather different state of affairs appears to prevail. Here three very closely allied species all belonging to the same genus, *Eucyclops*, have been studied, namely *E. agilis*, *E. macruroides* and *E. macrurus*. While a relatively small number of specimens of the last mentioned species have been examined and the results are therefore more subject to the element of chance than in the case of the other two, of which over a hundred specimens each have been examined, they are nevertheless worthy of consideration.

Table 2. *Percentage occurrence of the main foodstuffs of three herbivorous cyclopoids*

	Percentage occurrence		
	E. agilis	*E. macruroides*	*E. macrurus*
Filamentous green algae	49·0	47·0	37·5
Filamentous blue-green algae	6·6	3·6+1·8?	–
Colonial algae	17·9	25·9	9·4
Unicellular algae or broken colonies	32·1	28·6	15·6
Diatoms	67·0	66·0	50·0
Other algae	13·2	27·7	9·4
Animal matter	16·0	8·0	15·7
Indeterminate non-green mush	2·8	8·0	25·0

Table 2 shows the percentage occurrences of the various types of food found in the alimentary canals of these three species. A glance is sufficient to show that so far as the most important foods are concerned there is a remarkable similarity in the percentage of occurrences in the case of *E. agilis* and *E. macruroides*, and that *E. macrurus* also tends to feed largely on the same materials. Concentrating particularly on the first two species for which the evidence is especially strong, it would seem, therefore, that as both have almost identical food preferences, competition between them may be expected when they occur together. Of co-existence in nature there is undoubted proof for all three species have been found together among *Phragmites* at the margin of Esthwaite Water (English Lake District), and associated together under stones in the same lake (though *E. macrurus* was rare in this habitat). Attention has also been drawn to the association of closely allied species including *E. macruroides*, *E. agilis* and a subspecies of the latter, *E. a. speratus*, under single stones in a canal in Yorkshire (Fryer 1953). In addition *E. agilis* and *E. macruroides* have been collected on more than one occasion in a single sweep of a net.

Gut analyses of specimens of all three species collected among *Phragmites* at the same time in the month of December showed that all were feeding on similar algal foods, as were specimens of all three species found together under stones in the same lake. It would appear, therefore, that in spite of many statements to the contrary, some closely related animal species at least, of which the closely allied cyclopoid copepods *Eucyclops agilis* and *E. macruroides* constitute an example, can and do co-exist in the same habitat or even microhabitat and eat the same kind of food.

A recent study, the results of which are relevant to the present discussion, is that of Hartley (1953) working on the ecology of the English titmice, who found that usually the various species had special ecological preferences and hence in this case took somewhat different foods, but that at certain times the ecological separations between the different species disappeared. He was able to show that these extinctions of ecological separation coincided with temporary superabundance of food. The food of herbivorous cyclopoids appears to be almost always superabundant in nature and consequently food supply usually plays little part in controlling their numerical abundance. Competition for food between such closely allied species as those discussed above would therefore appear to be negligible, and as the feeding mechanism is the same in each case there seems no reason to suppose that interspecific competition for food is appreciably different from intraspecific competition. In these cases, therefore, it seems that purely physical conditions prevailing in the environment—temperature, chemical conditions, availability of shelter, etc.—coupled with dispersal efficiency and the ability to escape from predators may be far more important in determining the distribution of these species than are food requirements. As support of this suggestion, admittedly negative, can be quoted the absence of the almost ubiquitous *Eucyclops agilis* from moorland pools in an area of the Yorkshire Pennines, although it is exceedingly common in a diverse series of habitats studied in other parts of the area concerned. As pointed out elsewhere (Fryer 1955) apparently suitable food is often plentiful (and predators are absent), and one can only conclude that the physico-chemical characteristics of the environment restrict its occurrence.

In several cases where closely allied species occur together it has definitely been shown that ecological divergence has taken place in the form of differences in food and feeding habits, thus permitting co-existence without much competition. This has been shown to hold good for at least one pair of closely allied herbivorous freshwater calanoid copepods which co-exist in the plankton of Windermere (Fryer 1954). It is interesting to see that quite a different state of affairs appears to hold good in the freshwater cyclopoids. Hartley (1953) is only expressing a general opinion when he says: 'Only by the evolution of specialization of feeding habits are several closely allied species able to occupy and to exploit a single habitat.' This appears to be definitely untrue so far as some of the herbivorous freshwater cyclopoids are concerned.

FOOD PREFERENCES AND GENERIC AFFINITY

Studies on the food preferences of different species, when they concern such fundamentally different diets as those composed of plant and animal material, may help to throw light on the interrelationships and classification of cyclopoids at a generic level. The following discussion concerns a group of species in which this may be the case.

According to Kiefer (1929, and many subsequent papers) the five species which are here all referred to *Acanthocyclops* are placed in three genera or sub-genera, viz. *Megacyclops* (*A. viridis*), *Acanthocyclops* (*A. vernalis* and *A. venustus*) and *Diacyclops* (*A. bisetosus* and *A. languidus*). The morphological distinctions between these three groups are rather slender as Gurney (1933) has pointed out, but most continental workers have nevertheless followed Kiefer on the question of generic limits. While it must be admitted that the writer was originally biased in favour of Gurney's more conservative scheme, it must also be conceded that similarities and differences in food preferences of the five species of this particular group which have been studied indicate that Kiefer's scheme may merit support, particularly as recent studies on animal behaviour have shown that 'evolutionary relationships are often expressed even more clearly by similarities and differences [in behaviour] than they are by structures and morphological characteristics' (Thorpe 1954).

If all the species considered be regarded as constituting species of a single genus, then that genus must include both carnivores and herbivores. Such a state of affairs, while not unknown in nature, is distinctly rare. Now of these five species two are herbivores, and these two, *A. bisetosus* and *A. languidus*, are the two which, under Kiefer's scheme of classification, are placed in the genus *Diacyclops*. It seems, therefore, that in addition to possessing slight morphological distinctions, members of the group designated *Diacyclops* may be differentiated from *Megacyclops* or *Acanthocyclops* on the basis of dietary differences. Further studies on the diet of other representatives of the *Diacyclops* group are needed to confirm whether they are all herbivores but, basing supposition on their close affinity with *A. languidus* and *A. bisetosus*, upon the small size of the species concerned, and on the fact that they tend to live in very small bodies of water where plant material will often, or always, be much more readily available than animal food, it seems probable that they will prove to be herbivores. If this is indeed demonstrated then the genus *Diacyclops* will be shown to possess a degree of physiological as well as morphological uniformity.

The separation of *Megacyclops* and *Acanthocyclops* is not to be so readily seen from the scant evidence provided by *A. vernalis* and *A. venustus*, but there are some indications that the latter species takes some vegetable matter, which may indicate the beginnings of divergence in food habits as well as in morphology from the *Megacyclops* group.

As further studies on the food of other representatives of these debatable genera remain to be carried out in the future, it has been thought desirable for the purpose of this paper to regard them as members of the comprehensive genus *Acanthocyclops*, while yet recognizing that better grounds for their separation may now be imminent.

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SUMMARY

1. Carnivorous species include *Macrocyclops albidus*, *M. fuscus*, *Acanthocyclops viridis*, *A. vernalis*, *Cyclops strenuus*, *C. s. abyssorum* and *Mesocyclops leuckarti*.

2. Herbivorous species include *Eucyclops agilis*, *E. macruroides*, *E. macrurus*, *E. gibsoni*, *E. dubius*, *Acanthocyclops bisetosus*, *A. languidus* and '*Microcyclops*' spp.

3. The food of the carnivores includes crustaceans, dipterous larvae and oligochaetes, many of which are larger than the copepod preying on them, whilst the herbivores feed on a variety of algae ranging from unicellular diatoms to long strands of filamentous species.

4. The inability of cyclopoids to digest certain algae is pointed out.

5. Ecological implications of the feeding habits are discussed and the general role of freshwater cyclopoids in nature is reassessed.

6. The problem of competition for food by closely allied species is considered. While some divergence in food preferences seems to have taken place among closely allied carnivores this does not appear to be so among the herbivores. The latter apparently do not obey the so-called Gausian hypothesis which holds that closely related species cannot co-exist in the same ecological niche. Co-existence of closely allied herbivorous species seems to be associated with a superabundance of food in the habitats concerned.

7. Food preferences parallel morphological generic affinities and may assist in the realization of a natural classification of the Cyclopoida.

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SQUIRRELS IN ENGLAND, WALES AND SCOTLAND, 1955

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(With 1 Figure in the Text)

The distribution of grey squirrels (*Sciurus carolinensis*) and red squirrels (*Sciurus vulgaris leucourus*) in England and Wales during 1944-45 has been described in a previous paper (Shorten 1946). During 1950-52 a survey of their distribution was made in twenty-three counties and the West Riding of Yorkshire, and the results were given in another paper (Shorten 1953). It was noticed in 1945 that red squirrels tended to disappear from areas where grey squirrels had been present for at least fifteen years; and in 1952 it appeared that in eight counties red squirrels seemed to have disappeared from areas where grey squirrels had been established since 1945.

Records have been kept since 1952 of grey squirrels seen in areas not hitherto colonized by them. No countrywide survey has been made during this interval, except in forest areas belonging to the Forestry Commission. In 1954 a questionnaire was circulated to foresters in all Commission areas in England, Wales and Scotland, asking for information on the presence or absence of grey squirrels; this was followed in 1955 by a similar questionnaire in which information on both species was sought. In both years, more than half the forests lay outside the range of the grey squirrel. The results are summarized here, and a map is given for the distribution reported for each species in 1955 (Fig. 1).

I would like to thank all those foresters who supplied information, and the Forestry Commission staff at Alice Holt Forest Research Station and at Savile Row for their help in devising and circulating the forms; and also Mr F. A. Courtier (Alice Holt) who gave valuable assistance in the sorting, indexing and checking of results. Information on grey squirrels outside Commission areas came from members of the Country Landowners' Association, keepers, the Grey Squirrel (Scotland) Committee and the County Agricultural Executive Committees, to all of whom my thanks are due.

METHODS

Information on the continued spread of the grey squirrel since 1952 has been collected from surveys (1953-54; Grey Squirrel Enquiry, sent out by the Committee on Grey Squirrels to some 4000 foresters, keepers, landowners, squirrel clubs and others; 1954 and 1955: questionnaire on squirrel damage, sent to all Commission

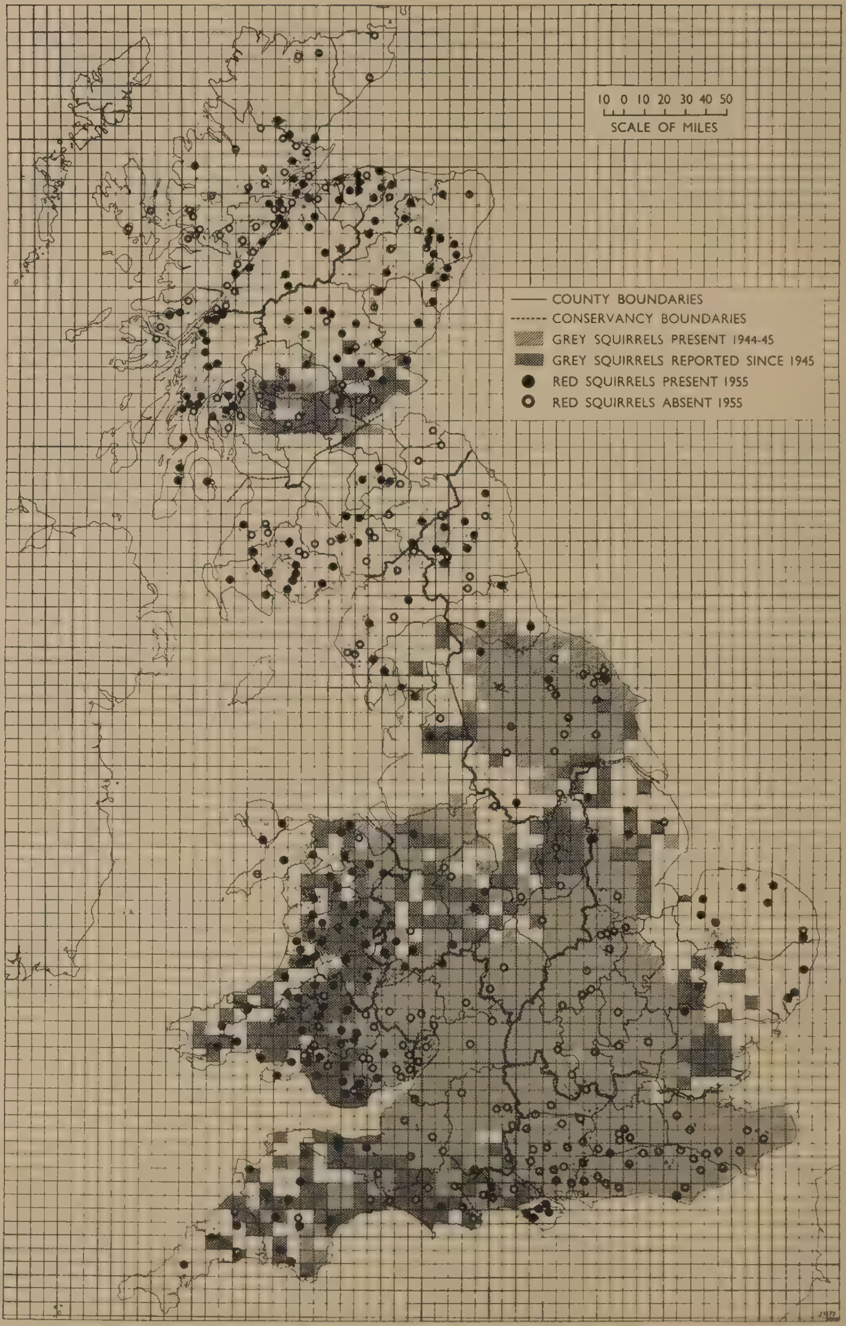
10 0 10 20 30 40 50
SCALE OF MILES
COUNTY BOUNDARIES
CONSERVANCY BOUNDARIES
GREY SQUIRRELS PRESENT 1944-45
GREY SQUIRRELS REPORTED SINCE 1945
RED SQUIRRELS PRESENT 1955
RED SQUIRRELS ABSENT 1955

Fig. 1. The distribution of grey squirrels in England, Scotland and Wales from 1945 to 1955, and the distribution of red squirrels as reported from Forestry Commission areas in 1955. Map drawn by A. G. Jenson, M.A.F.F., Tolworth.)

forests) and from reports made through County Pests Officers and by private individuals from February 1954 to December 1955. Where grey squirrels were reported to be present, the National Grid (10 km) square concerned was marked as positive. No attempt was made to fill in the gaps between such records, and grey squirrels may have been present in some areas that were not covered. In the same way areas which had previously reported the presence of grey squirrels were not surveyed systematically to confirm that squirrels were still present, but only nineteen forests lying within such areas in the whole of England, Wales and Scotland failed to confirm their presence.

Commission foresters were asked to say whether grey squirrels were numerous or scarce in 1954 and 1955, and were also asked to say whether numbers were more or less in 1955 than in the preceding year.

Table 1. *Grey squirrels in Commission forests, 1954*

Conservancy	Total no. forests	Grey squirrels absent	Grey squirrels		Total with squirrels
			Scarce	Numerous	
England (NE)	40	20	17	3	20
(NW)	35	18	17	0	17
(E)	48	28	15	5	20
(SW)	46	9	30	7	37
(SE)	35	1	23	11	34
New Forest	3	2	0	1	1
Dean	13	0	7	6	13
Total	220	78	109	33	142
Wales (S)	47	8	31	8	39
(N)	34	15	17	2	19
Total	81	23	48	10	58
Scotland (N)	51	51	0	0	0
(W)	33	25	7	1	8
(S)	41	41	0	0	0
(E)	43	38	5	0	5
Total	168	155	12	1	13
Grand Total	469	256	169	44	213

The presence or absence of red squirrels was recorded from 538 Commission areas in 1955, and foresters were asked to state whether red squirrels were numerous or scarce, and whether numbers were greater or less than in 1954.

Results are given in Tables 1 and 2, and in Fig. 1. The number of forests for which information is given in Table 2 is greater than that plotted in Fig. 1, since some units of large forests have been counted as separate areas.

RESULTS

(a) *Grey squirrels*

A map of Forestry Commission areas reporting grey squirrels to be present in 1954 revealed that several advances had apparently been made since the last survey in 1952. In Montgomeryshire, Mathrafel, Hafren and Tarenig reported their presence; in Merioneth they were to be found at Hafod Fawr, and one had been seen at Dovey Corris; in Cardiganshire they were at Cwmeinion; in Denbighshire six were said to have been seen within the forest area at Clocaenog; in Glamorgan

Table 2. *The distribution of squirrels in Commission forests, 1955*

Conservancy	Total forests	Squirrels absent	Red squirrels only			Grey squirrels only			Forests with both species present				
									Red		Grey		Total
			Numerous	Scarce	Total	Numerous	Scarce	Total	Numerous	Scarce	Numerous	Scarce	
England (NE)	42	8	–	18	18	1	13	14	–	2	–	2	2
(NW)	35	13	–	7	7	–	6	6	–	9	–	9	9
(E)	51	2	17	12	29	1	16	17	–	3	–	3	3
(SW)	48	5	–	8	8	3	22	25	–	10	1	9	10
(SE)	44	4	–	1	1	2	37	39	–	–		–	–
New Forest	13	–	–	2	2	4	6	10	–	1	–	1	1
Dean	13	–	–	–	–	–	13	13	–	–	–	–	–
Total	246	32	17	48	65	11	113	124	–	25	1	24	25
Wales (S)	55	4	1	9	10	4	13	17	7	17	1	23	24
(N)	35	2	3	16	19	–	–	–	3	11	3	11	14
Total	90	6	4	25	29	4	13	17	10	28	4	34	38
Scotland (N)	61	38	–	23	23	–	–	–	–	–	–	–	–
(W)	45	11	1	22	23	1	2	3	–	8	–	8	8
(S)	42	17	1	24	25	–	–	–	–	–	–	–	–
(E)	54	11	1	40	41	–	1	1	–	1	–	1	1
Total	202	77	3	109	112	1	3	4	–	9	–	9	9
Grand Total	538	115	24	182	206	16	129	145	10	62	5	67	72

three had been seen in the last two years at Rheola; in Carmarthenshire they were found to be present at Brechfa. New records in England included Corvedale and Habberley in Shropshire, Oakamoor and Bagot in Staffordshire, Willingham in Lindsey (Lincs.), Doncaster Forest in Yorkshire and Molton Woods and Halwill in Devon. At Molton Woods infiltration by grey squirrels had just begun, and red squirrels were said to be common. In Scotland grey squirrels were said to be present but scarce in three forests beyond the known range: at Tentsmuir (Fife), Strathyre (Perth) and Rowardennan (Stirling).

In 1955 they appear to have spread to Coed Penllyn in Merioneth, St Fillans in Perthshire, Minard in Argyll, near Selm Muir in Midlothian and to Hartland in south-west Devon.

Twenty-four areas reporting grey squirrels present in 1954 reported them absent in 1955. These were:

Buckinghamshire	Bucklebury
Devonshire	Halwill, Dartmoor, Lydford and Fernworthy
Leicestershire	Charnwood
Lincolnshire, Kesteven	Willingham
Shropshire	Causeway Wood
Yorkshire	Londesborough, Tong Woods and Doncaster
Brecon	Irfon and Taf Fechan
Carmarthen	Brechfa 3 and 5
Flint	Coed Clwyd
Glamorgan	Penllergaer and St Gwynno
Merioneth	Dovey Corris and Hafod Fawr
Montgomery	Tarenig
Fife	Edensmuir, Pitmedden and Tentsmuir

Thus grey squirrels apparently disappeared from some of the recently colonized areas in 1955.

In 1954, 256 areas out of the 469 replying stated that grey squirrels were absent, 169 reported them to be scarce, and forty-four reported that they were numerous; but in 1955, 321 out of 538 reported them to be absent, 196 reported them to be scarce, and only twenty-one reported that they were numerous. The latter group included:

Devonshire	Haldon
Hampshire	Bramshill; Fritham, Parkhill, Rhinefield and Stockley (New Forest)
Herefordshire	Aconbury
Northamptonshire	Salcey
Sussex	Marden
Wiltshire	Bentley
Yorkshire	York
Brecon	Glasfynydd
Glamorgan	Coed Caerdydd
Monmouth	Llanover, Tintern South and Nethergwent
Montgomery	Mathrafal, Carno and Bechan
Dunbartonshire	Garelochhead

Of 150 forests in which the density of grey squirrels in 1955 was compared with that observed in 1954, ninety-six reported it to be less, thirty-five reported it to be the same, and nineteen (fifteen of which were in Wales or south-west England) reported it to be greater.

As a result of the 1953-54 Enquiry, thirty-four new grid squares were found to include localities reporting grey squirrels; and in areas where the species was already established its continued presence was confirmed in 215 squares.

The new records of grey squirrels in 1953-54 were from:

Cardigan	Newquay, Capel Bangor, Llanrhystyd, Penglais Wood (near Aberystwyth), near Cardigan, Llanarth and Llanyssul
Montgomery	Vyrnwy, Llanfair Caereinion, Llandinam, Llanidloes and Carno
Shropshire	Shifnal, Shavington, the Acton-Reynold estate near Shrewsbury, Cross Houses, High Hatton, Calvington, Cressage Park and the Wrekin
Derby	Osmaston, Radburne, Eckington Wood and Renishaw Park
Merioneth	Llanderfel, Llanfachreth
Lancashire	Downham and the Stonyhurst estate
Devon	Affeton estate and five miles north of Barnstaple
Somerset	Williton and West Quantoxhead
Sussex	Udimore
Lincolnshire	Scawby
Leicestershire	Shenton
Staffordshire	Oaken Codsall, Brereton, Ranton and Ellenhall

Mr D. A. Woodburn, Secretary of the Grey Squirrel (Scotland) Committee, provided the following records for Scotland in 1954:

Dunbartonshire	Auchentoshan; half a mile east of Old Kilpatrick; Mains; one mile north-east of Balloch; Cameron (Bonhill); Auchengower; Cumbernauld
Stirling	Half a mile south of Drymen; Finnich Glen; one mile west of Blanefield; half a mile south of Blanefield; Craigmaddie; Lennox Castle; Torrance; Leckie; Touch; Torwood; Sauchieburn; Bannockburn; Dunmore Park
West Lothian	Torphichen; Bangour; half a mile west of Livingstone station; half a mile south of Drumshoreland station
Fife	Bogside; Inverkeithing; Donibristle; Raith House; Chapel; Leslie; E. Wemyss; Markinch; Falkland House; Lathrusk House; Collessie; one mile north-west of Kirton of Largo; Balcarres House
Kinrosshire	Blairadam; Cleish
Perthshire	Dupplin Castle; Commonedge Hill; Cowden Castle; Glendevon; Ochtertyre; Rhynd; Rednock; Invertrossachs; Farmston; Muckle Burn

Records from County Agricultural Committees and others, collected between 1952 and 1955, are summarized below:

Lancashire	Pendle Hill; Winkley Hall (1954)
Yorkshire	Welton area (1955)
Lincolnshire	Wroot (1954); Legbourne; Ludford; Bishopsthorpe area (1955)
Cambridgeshire	Wilbraham Hall (1952)
West Suffolk	Norton; Great Thurlow; Layham (1954); Lawn Wood; Littley Wood; Withersfield (1955)
Norfolk	Thetford Warren (1954); one mile from Lynford Hall (1955)
Essex	Wickford; Billericay; N. Fambridge; Galleywood; Stisted; Shalford; Warley (1954)
Somerset	Croydon Hall (1953)
Cornwall	Cartha Martha; Bodmin; Duloe; St Neot; Congdon; Lewannick; St Thomas; Canworthy Water; Jacobstow; Boscastle (1955)

These records suggest that since 1945 grey squirrels have advanced over a broad front into both North and South Wales, being found at points up to sixty miles west of those known to have been colonized before. They have overrun the south-west areas of Dorset and Somerset, and scattered foci in Devon have linked up. In 1955 grey squirrels entered Cornwall for the first time; and there has been a further spread within the counties of Cheshire, Shropshire, Staffordshire, Derby and Nottinghamshire. They were reported in Westmorland and in the Clitheroe area in Lancashire; in Lincolnshire there were sporadic records in the Lindsey Division, and a slight eastward spread in Kesteven. The eastward movement was most marked in Essex, where it covered some twenty miles. From northern Essex and eastern Cambridgeshire it appears that attempts were made to enter west Suffolk and Norfolk; it will be interesting to see if a passageway has now been found across the unexplained barrier which seems to have prevented any spread into these counties until recently. In Scotland the more recent and complete records available show that grey squirrels are to be found over more than twice the area where they were known to be in 1945. The western and eastern centres of introduction have joined up; and there has been a spread eastwards across Fife, and northwards into Perthshire.

(*b*) *Red squirrels*

Of the 538 Commission forests surveyed in 1955, 260 were said to be without red squirrels, 244 were said to have red squirrels present but scarce, and in thirty-four they were said to be numerous. The latter were as follows: Norfolk: Croxton, Santon, Methwold, Downham, Harling, West Tofts, Lynford, Cranwich and Hockham (all beats of Thetford Chase); Swaffham. Suffolk: High Lodge, Elveden, Redneck and Mildenhall (Thetford); The King's and Rendlesham. Cambs.: Ditton. Carm.: Caio,* Crychan,* Llandeilo,* Brechfa 2,* Brechfa 4,* Pembs.: Teifi* and Daugleddau. Cards.: Towy. Mont.: Dovey Corris, Dovey Bryncynfil, Dovey Valley,* Commins Coch. Merioneth: Coed Penllyn.* Radnor: Coed Sarnau.* Arran: Glenrickard. Wigtown: Kilsture. Fife: Tentsmuir.

Seventy-two forests claimed to have both species of squirrel present; thirty-eight of these were in Wales, ten in south-west England, nine in north-west England, and eight in west Scotland. Most of the forests concerned had been colonized by grey squirrels within the last ten years. Only five forest areas reporting grey squirrels to be numerous also had red squirrels present: these were: Haldon (Devon), Coed Caerdydd (Glam.) and Mathrafal, Carno and Bechan (Mont.). In these forests red squirrels were said to be scarce.

In England and Wales, roughly 20% of the forests falling within the 1945 distribution of grey squirrels reported red squirrels present in 1955; and these areas were almost all on the fringes of the 1945 range, so that the particular habitats of the red squirrels may not have been invaded until later. In Wales, for example, red squirrels are still to be found in many districts entered by grey squirrels since 1945, but are absent from parts of Brecon and Monmouthshire where the greys were already established by that time. It must be remembered, however, that only the Commission areas were surveyed; red squirrels may have been present within a grid square, but absent from Commission ground within that square. It has also been assumed that the character of the forests within and without the 1945 range of the grey squirrel does not vary so grossly as to affect the red squirrel distribution.

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* These forests also had grey squirrels present, but scarce.

The absence of red squirrels from forests within a considerable area of north-west Scotland is interesting, if the Forestry Commission areas there represent a fair sample of the local woodlands. Only seven cases (ignoring Sutherland and Caithness) can be explained by the absence of trees more than twenty years old; it has been suggested that the absence of red squirrels may be correlated with the high rainfall suffered in the area, and the scarcity of Scots pine.

The density of red squirrels was compared with that of the preceding year on 145 areas. In forty-eight it was said to be less, in seventy-seven the same, and in twenty it was said to be greater. If these judgments are assumed to be accurate, and if the conditions in Commission forests are taken as representative of the majority of woodland areas, then it suggests that the red squirrel population suffered less than did the grey during 1954-55. Red squirrels were said to be present in 278 forest areas in 1955, whereas greys were only recorded in 217 areas.

SUMMARY

1. Records of grey squirrels seen in new areas since 1952 have been collected, and in 1955 information on the presence or absence of both red and grey squirrels was gathered from 538 forest areas.

2. Of the forests 115 had neither species, 145 had grey squirrels only, 206 had red squirrels only, and 72 had both species. In England and Wales roughly 80% of forests lying within the 1945 range of the grey squirrel had no red squirrels in 1955; the remainder lay near the fringes of the 1945 range. Most forests reporting that both species were present had been colonized by greys since 1945.

3. In England the grey squirrel population in Yorkshire and that in Nottinghamshire and north Lincolnshire are now separated by less than ten miles, Cornwall has been entered, and Norfolk and west Suffolk seem about to be colonized. Advances of up to sixty miles have been made across Wales, and in Scotland the distribution has spread over twice the area known to have been covered in 1945. A reduction in the number of grey squirrels present was noticed in many areas in 1955.

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THE SALINITY CHARACTERISTICS OF THE MIDDLE AND UPPER REACHES OF THE RIVER BLYTH ESTUARY

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(With 7 Figures in the Text)

INTRODUCTION

The distribution of free-living nematodes inhabiting the intertidal muds of the Blyth estuary has been studied in relation to salinity distribution. This paper presents the results of the investigations into the salinity variations in both the tidal water of the estuary and the interstitial water of its muds, while the distribution of the free-living nematodes will form the subject of a later paper.

In this country the salinity conditions in the estuary of the River Tees (Alexander, Southgate & Bassindale 1935), the estuary of the River Severn and the Bristol Channel (Bassindale 1943*a*, *b*), and the River Tamar (Cooper & Milne 1938, Milne 1938, 1940, Percival 1931, Spooner & Moore 1940) have been studied in detail. The River Blyth estuary is much smaller than any of these, and only the general principles found in the larger estuaries can be applied to it. Day (1951) and Yonge (1949) give reviews of these general estuarine conditions.

The distribution of free-living nematodes in water of varying salinity has been the subject of much research in the Baltic Sea and in certain areas of the Zuiderzee, while in this country Rees (1940) has dealt with free-living nematodes as part of a larger study of the ecology of a mud flat in the Bristol Channel. Bassindale (1943*b*, p. 3) has pointed out that 'it has long been known that if the salt content of the water in which they live is changed sufficiently slowly, many animals can acclimatize themselves to large changes. Thus although the magnitude of the change is important, the rate of change is also significant'. In the Zuiderzee and Baltic, rates of salinity change are much less rapid than those found in estuaries, and the distribution of nematodes under conditions of high rates of change has not previously been studied.

Nematodes live in the interstitial water of the mud, and Rees (1940) has shown that the greater part of this constituent of the microfauna is concentrated in the surface 2 cm of intertidal mud. It was therefore necessary to investigate salinity conditions in the interstitial water near the surface of the mud. Reid (1930, 1932), Alexander *et al.* (1932) and Smith (1955) have worked on the salinity of interstitial water in mud and sand, and all have found that salinity conditions tend to be more stable with increasing depth, and that salinities could be maintained at a high level—varying with depth—below nearly fresh overlying water at low tide. Reid states that '. . . marine burrowing animals living in estuaries are in no way affected by the presence of overflowing fresh water at low tide provided they can burrow to a depth of 12 in. Only the animals which live in the surface have to be capable of adapting themselves to varying conditions, as shown by Pantin (1931)'.

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In intertidal muds, which are exposed twice a day at low tide, salinity variations due to the evaporation of water from the mud might, however, be an important factor. Alexander *et al.* (1935) found no appreciable change in the salinity of interstitial water in the Tees when it was uncovered during the ebb tide, but it is hard to reconcile this finding with the fact that salt is seen to crystallize on the surface of exposed mud in the Blyth estuary during the summer months. Nicol (1935), during a study of brackish water pools in a salt marsh, found that evaporation of water from the pools eventually exposed the mud to the action of sun and wind; salinities in the mud were then profoundly altered by evaporation. Values of up to 60 g Cl/litre were recorded during one period of drought. In this habitat such high values were only reached occasionally when the mud in the pools was exposed, while in estuaries with large areas of intertidal mud, exposure occurs twice in 24 h. It was not known what effect exposure would have on the interstitial water in such cases, and this factor has therefore been studied in some detail.

DESCRIPTION OF THE ESTUARY

(*a*) *General*

The River Blyth opens to the North Sea on the coast of Northumberland 8 miles north of the River Tyne. Most of the coal shipped from the Northumberland coalfield is exported from the Port of Blyth. 5,382,900 tons of coal were exported in 1954, while total imports, consisting mainly of cement and pit props, only amounted to 71,000 tons. The history and development of the port has closely followed that of the coalfield it serves, and the loading facilities of the harbour have been greatly increased since 1900. By 1912 the harbour had been deepened throughout to 24 ft below Admiralty Chart Datum (ACD). To make this improvement 500,000 cu. yd of rock were removed from the river bed. Continuous dredging is necessary to maintain this depth, and the Harbour Commissioners estimate that 200,000 tons of silt are removed by dredging each year. The length of the estuary, from the L.N.E.R. viaduct to a point between the two entrance piers, is 3·8 miles, but at spring tides the river is often tidal above the viaduct. However, the depth of the water at this point never exceeded 6 ft on the spring tides used in the horizontal salinity surveys, and for the purpose of this account the viaduct is assumed to be the upper limit of the estuary.

Day (1951) discusses the division of estuaries into head, upper reaches, middle reaches and mouth or lower reaches by means of salinity variations encountered along the length of the estuary. In the Blyth, salinities ranging from almost fresh (1 ‰) to almost salt (33-35 ‰) may be encountered above the harbour installations at certain times of the year, and salinity has been used only as a rough guide to these divisions. Fig. 1 shows the middle and upper reaches; the part of the estuary with which this work is concerned. A preliminary survey showed that the largest salinity changes took place in this region of the estuary, and because of this factor and the artificial nature of the channel in the harbour, it was decided to restrict this investigation to the middle and upper reaches (cf. Alexander *et al.* 1935, p. 720). No further salinity determinations were made in the lower reaches.

It will be seen from Fig. 1 that the estuary is formed by the union of two arms. A small stream, the Sleekburn, enters the northern arm, while the River Blyth runs in the more southerly branch. The estuary can be split into four distinct regions: the upper reaches of the River Blyth, the narrow Sleekburn, the wider and deeper middle reaches, and finally the harbour or lower reaches. The estuarine deposits of the intertidal area fall into these divisions. Apart from the strip of gravel which runs between MHWS and MHWN, the middle and upper reaches have quite different deposits. The upper reaches are characterized by extensive areas of soft mud, occasionally broken by stones covered with *Fucus*. The middle reaches have a wide range of different deposits: clean sand, sand and mud, sand and gravel, soft black mud, soft mud with gravel and *Mytilus* shells, and some patches of clay are to be found in this region. The bottom deposit in the lower reaches is predominantly soft black mud, but a relatively small area is exposed because of the wharves and quaysides.

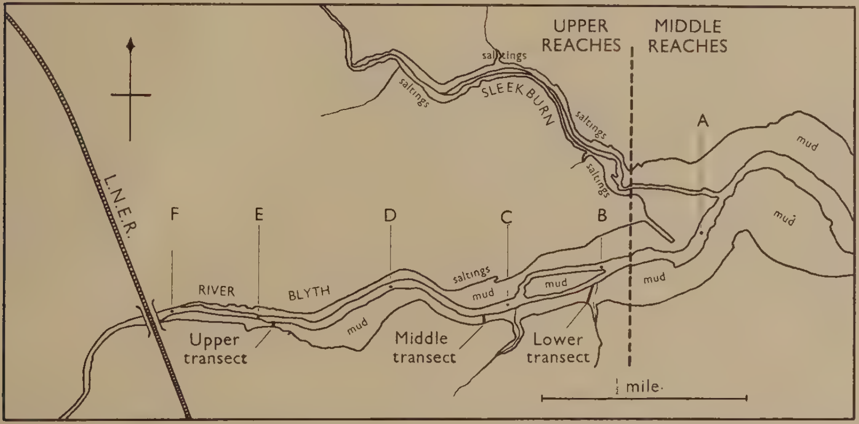

Fig. 1. Sketch map of the middle and upper reaches of the Blyth estuary, showing the salinity stations used in the horizontal surveys and the position of the three transects.

The shallow upper reaches are drained at low tide, when the River Blyth is restricted to a narrow channel running between extensive areas of mud. Most of the mud slopes evenly towards the river channel, and apart from one exception at the south side of the middle reaches, mud 'flats', in the strict sense, do not occur. The bottom at salinity station A in the middle reaches is 2 ft below ACD, while at salinity station F at the head of the estuary it is 8·5 ft above ACD. Thus the deposits of the upper reaches and the greater part of the middle reaches lie above ACD, so that the lowest sampling point on any one transect is 3·8 ft above ACD, enabling periods of up to four hours' exposure to be obtained along the whole length of the transects. As the river channel gradually rises towards the head of the estuary, a decreasing proportion of the intertidal deposit lies below mid-tide level, until at a point just below the viaduct the channel bottom is actually 1 ft above mid-tide level.

Surrounding the shallow basin of the estuary is an earth 'cliff' 2-10 ft in height, which is gradually being undermined in places and collapsing on to the strip of gravel running beneath. This low cliff extends up the gullies on the south side of the upper reaches. One small sewer outfall enters the channel at low tide slightly above salinity station E, and a small volume of untreated sewage is discharged into the streams which enter the channel at salinity stations B and C. As far as the middle and upper reaches are concerned, no signs of oxygen deficiency resulting from sewage outfall have been detected. The characteristic smell of hydrogen sulphide usually present in oxygen deficient muds was not noted after careful investigation near the sewer, or at any of the other positions examined.

(*b*) *Lower transect* (Grid ref. 2957/8236 Bearing 18° E of true N)

The lower transect is 280 ft long, considerably longer than the other two. As it covers approximately the same vertical distance as the middle transect, the angle of slope is much smaller. The substratum consists entirely of soft mud, and stones do not interfere with sampling. A profile section of the transect is shown in Fig. 2, and the positions of the transects in Fig. 1. In the summer months a pad of *Enteromorpha* spp. covers the mud from about 5·5 to 11 ft above ACD. The distribution of this species is not uniform, and in localized areas within these limits it is absent altogether.

(*c*) *Middle transect* (Grid ref. 2918/8227 Bearing 5° W of true N)

This transect is 90 ft long, extending from the lower edge of the gravel strip to the river channel. The transect slopes more steeply than either of the other two, falling from 11·9 to 2·8 ft above ACD in 90 ft (Fig. 2). The substratum is predominantly mud, with scattered stones covered with *Fucus* spp. The upper two sampling areas have some gravel mixed with the mud, which tends to interfere with sampling. In the summer months *Enteromorpha* spp. is most abundant on the upper two sampling areas, becomes more dispersed between 10·3 and 6·5 ft above ACD, and is absent altogether from lower levels. As on the lower transect, the distribution of this species is not uniform.

(*d*) *Upper transect* (Grid ref. 2825/8225 Bearing 6° E of true N)

This was established as near as possible to the head of the estuary. It is 90 ft long, falling only a vertical distance of 6·2 ft (Fig. 2). The upper limit of the transect is slightly higher than the middle or lower transects, while the lower limit is considerably higher due to the rise in the river bed. The substratum is predominantly mud, with a few scattered stones with some *Fucus* spp. As on the middle transect the upper two sampling areas have some gravel mixed with the mud. *Enteromorpha* spp. is not present. Sampling areas and interstitial salinity stations are

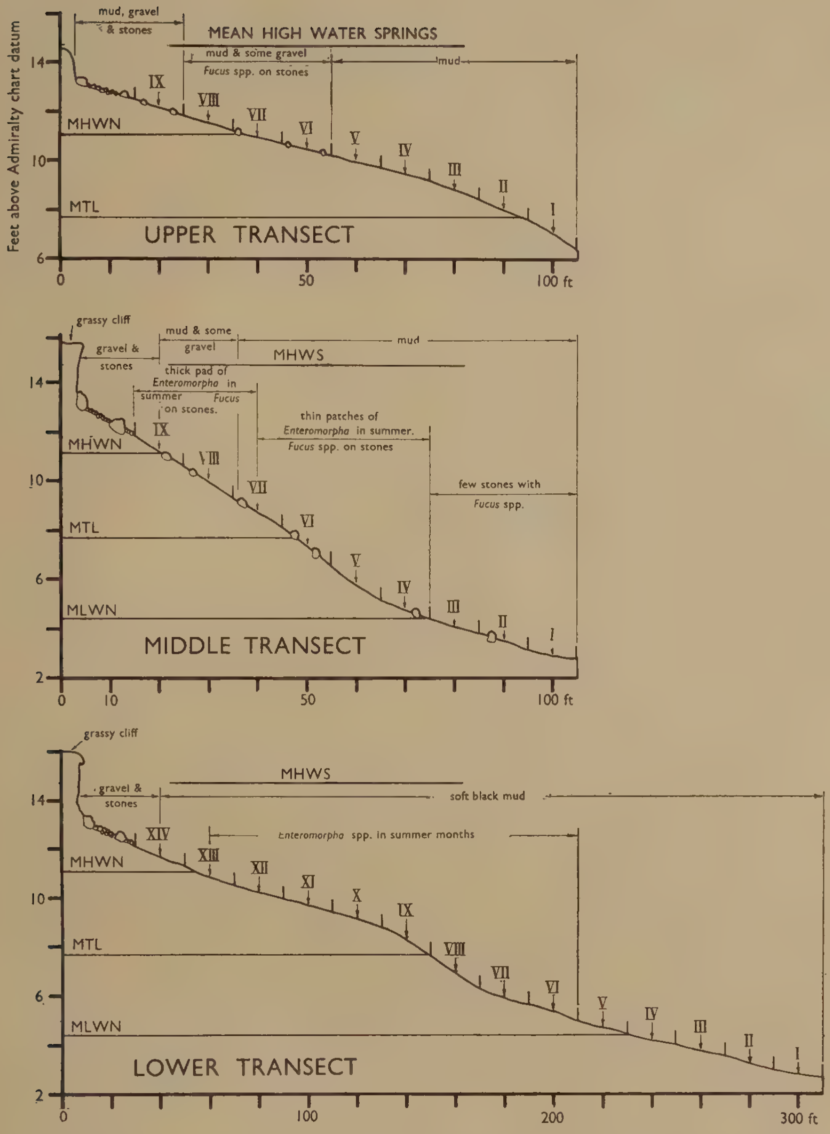

Fig. 2. Profile sections of the transects showing the position of the interstitial salinity stations (arrows and Roman numerals), and the vertical boundaries of the ecological sampling areas (vertical lines on the mud surface).

shown for each transect in Fig. 2. The latter were marked by numbered metal pins placed 20 ft apart on the lower transect and 10 ft apart on the middle and upper transects. These markers were taken as the centre of the ecological sampling areas, which were 20 × 6 ft on the lower, and 10 × 6 ft on the other transects. The horizontal boundaries of the sampling areas were not permanently marked but were laid down with a length of cord before sampling.

METHODS

(a) *Estuarine water*

All salinity titrations were made with the same portable apparatus, consisting essentially of a box containing a burette fitted with a side arm and siphon, using a glass bead in rubber tubing instead of the more conventional tap. 5 ml of the sample was titrated immediately against silver nitrate solution previously standardized against standard sea water (*eau de mer normale*) of stated chlorinity, using 5% potassium chromate as indicator. Burette readings were to the nearest 0·05 ml, and the salinity in g/kg or ‰ was obtained from Knudsen's Tables (1901) to the nearest 0·1 ‰.

(b) *Interstitial water of muds*

Reid (1930, 1932) working on the salinity interchange between salt water in sand and overflowing fresh water at low tide, used a graduated pipette fitted with a rubber bulb for the collection of interstitial water. Smith (1955) used the same method for the interstitial water of Kames Bay, Millport. Alexander *et al.* (1932) collected interstitial water from intertidal mud by digging a hole 6 in. deep and allowing the water to percolate into the hole. Nicol (1935) removed a core of mud, removed excess water and divided each sample into two halves. One was weighed, dried to constant weight and reweighed, the other was washed free of chloride with distilled water and the amount of chloride estimated by titration with silver nitrate. The salinity of the interstitial water was then calculated. The pipette method of obtaining interstitial water was tried and found to be a failure, as the soft mud completely blocked the aperture. The method used by Alexander *et al.* (1932) was no more successful, as the greater part of the water filling the hole originated from the surface of the mud. The method used by Nicol (1935) was considered to introduce inaccuracies arising from the leaching of halogen ions from the fauna within the mud, and furthermore was very time-consuming.

A mud sledge was therefore designed which would overcome the problem of surface water and collect mud at a required depth (Fig. 3). As the greater part of nematode populations are found in the surface 2 cm of intertidal mud (Rees 1940), the sledge was designed to collect at a depth of 0-2 cm. When the sledge was pulled gently along the surface of the mud, a ribbon of mud 15 × 2 cm was passed backwards on to its body. Most surface water was expressed from beneath the sledge by the flat region in front of the cutter, while any that remained on the ribbon drained rapidly away. The ribbon was not used until a few minutes after collection, by which time no further water drained from it. About 400 ml of mud were removed from the sledge with a trowel and pressed firmly into one of twelve plastic filter funnels supported by a wooden rack. Each funnel was of 12·5 cm diameter, and contained a sheet of Whatman's No. 1 filter paper. With most muds sufficient water for a salinity titration (5 ml) drained into a boiling tube in 5 min, but in some cases where the water content was low, as long as 1 h was required. In such cases the funnel was covered and the mouth of the boiling tube packed with cotton wool to prevent evaporation. From nine to twelve samples were collected from the interstitial salinity stations on the transect within half an hour. Each sample was placed in a funnel a few minutes after collection. The time taken to collect, drain and titrate twelve samples rarely exceeded 2 h.

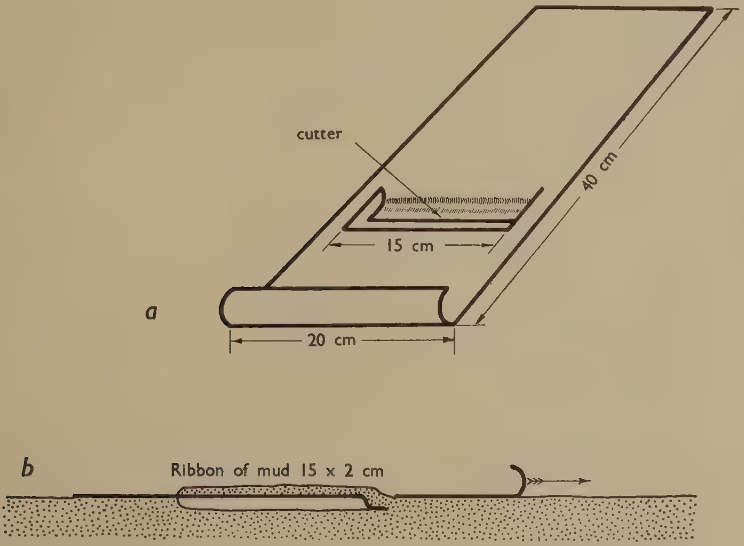

Fig. 3. The mud sledge: *a*, from the front and above; *b*, section showing the sledge in action.

The following method was adopted to give a fixed number of hours' exposure over the whole length of the transects. Two series of samples were taken on each occasion; the first always started 2-2½ h before the predicted time of low tide. If, for instance, the effect of four hours' exposure was required, the first series would be started 2 h and finished 1½ h before low water, while the second would be started 2 h and finished 2½ h after low water, working the same way along the transect. This procedure ensured that each sampling point was sampled after a fixed number of hours' exposure, and the results for each survey were made comparable by starting the first series at a fixed time before low tide. The point is important, as it ensured that any particular interstitial salinity station, at a given height above ACD, had been exposed for the same period before the first series of samples was taken.

During the periods of exposure studied, the relative humidity, the temperature of the air and surface 1 cm of mud were recorded every hour or half-hour.

(*c*) *Intertidal levels*

The soft nature of the mud excluded the use of orthodox surveying methods for determining the heights of the interstitial salinity stations above ACD. After some preliminary observations on tides it was decided to use the water level of a flood tide to determine the relative heights of these points, and, if it proved feasible, the absolute levels.

The river water becomes piled up at the head of the estuary producing slight differences in the height of the tide over the estuary as a whole, and makes the ebb tide somewhat longer than the flood. The flood tide is least affected, and was therefore chosen for the survey. The relative heights of the tide at one time were assumed to be identical at all three transects, which fall within a distance of 0·7 miles. A windless day was chosen, and an observer stationed on each transect. The time the water level reached each interstitial salinity station was noted on synchronized watches. A tide curve was drawn for the particular tide using the Admiralty Tide Tables (1949-52), and the curve from the tide recorder in Blyth harbour as a general guide to shape. The height of each position on the transect was read off from the curve which was related directly to ACD. Final results were checked by comparison with Supplementary Table I in the Admiralty Tide Tables, and they were found to agree within ±0.1 ft. The position of MLWN, MTL, MHWN and MHWS, are those given in Supplementary Table V for the River Tyne. Calculated mid-tide level on the middle transect was compared with the mid-tide level at the tide recorder on two other windless days, and all were found to agree within 4 in. Provided the weather is calm and observations are made on the same tide, this procedure would therefore appear to be quite accurate, and any errors would be constant for each transect. Evans (1947) reports a surprising measure of agreement between results, applied to the intertidal zonation of algae, made by this method and those obtained from detailed levelled traverses in the Plymouth area. It is doubtful whether orthodox surveying on soft mud would have produced such accurate results.

THE VERTICAL DISTRIBUTION OF SALINITY

Tidal cycle surveys were carried out once every 3 months from a boat moored at salinity station C. Two factors influenced the selection of the tidal cycles for these surveys. Firstly, as a boat was required from the beginning of the twelve-hour cycle, high water had to be in the early morning, and secondly it had to be of sufficient height to allow free passage up the estuary from the harbour. The dates, and an analysis of the tidal heights, are given in Table 1. The boat was in position as near as possible to the time of high water in the morning. Care was taken to assure that it was moored in the same position for each survey, and that it was carefully maintained in position during the rise and fall of the tide. Water samples were taken with a Casella water sampler from the bottom and the surface 3 in. every half-hour during the twelve-hour cycle. When the estuary was completely drained of tidal water, and the river channel maintained a constant level at 2 ft, only surface samples were taken.

The results of these surveys are shown in Fig. 4. They show that the River Blyth estuary is characterized by a vertical salinity gradient, and that the difference in salinity between surface and bottom water is greatest at high tide. A considerable quantity of fresh water entered the estuary in March, September and December, but very little in June. In the former months the fresh water remained discrete on the surface before and after the time of high water, and only underwent mixing with the more dense bottom water at the beginning of the flood and at the end of the ebb tide, when depths were decreasing and the two layers approached one another. The mixing resulted in the salinity of the surface layers being raised, and that of the bottom water being lowered. In September and March the degree of mixing was more thorough during the flood tide than during the ebb. This held for June, although very low salinities were not encountered, and would probably have been the case for December had not the temperature of the surface water been approaching freezing point, considerably lowering the density of this layer. The greatest temperature difference between surface and bottom water was recorded in December, and these differences were larger during the flood than during the ebb tide. It is suggested that in December the combined effect of low temperature on density, and the large volume of river water, allowed the 'fresh' surface water to remain relatively undisturbed during the normal mixing period in the first half of the flood tide. A small rise in the salinity of the surface water did occur in this month, <1-7·45‰, 1430-1600 h, an indication of some mixing, but this was much less than in March (3·5-30·5‰, 1430-1600 h) and September (<1-28·5‰, 1530-1800 h).

Table 1. *Tidal cycle surveys: dates and heights*

		Height of tide (ft above ACD)	Range of ebb and flood (ft)	Mean range (ft)
12 Mar. 51	HW	13·2		
	LW	1·5	11·7	12·10
	HW	14·0	12·5	
5 June 50	HW	13·8		
	LW	1·7	12·1	11·50
	HW	12·6	10·9	
1 Sep. 50	HW	14·5		
	LW	1·4	13·1	12·35
	HW	13·0	11·6	
13 Dec. 50	HW	14·2		
	LW	2·4	11·8	11·85
	HW	14·3	11·9	

From these surveys it is possible to obtain a general idea of the periods when the large body of bottom water was subject to large and rapid changes in salinity, and which region of the middle transect was affected by these variations. The

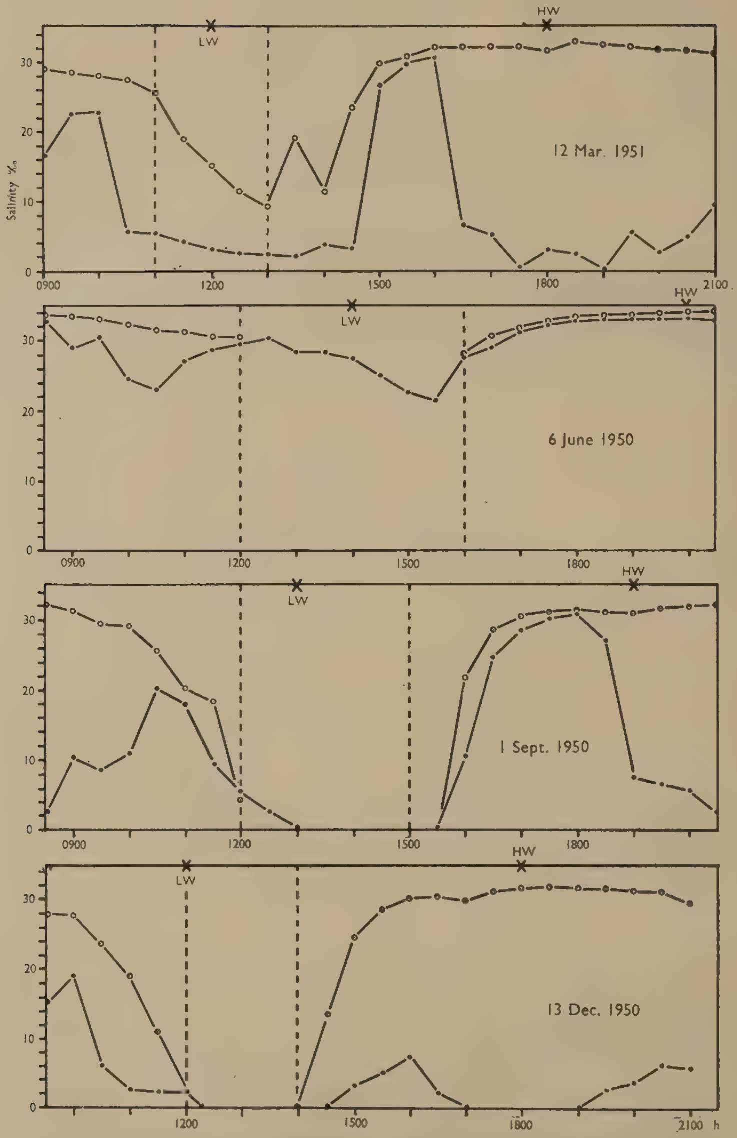

Fig. 4. The salinity of the surface and bottom water during the twelve-hour tidal cycle. Surface water ●-●-●, bottom water o-o-o. Dashed lines show the times when the estuary at salinity station C, was drained of tidal water and the river channel maintained a constant depth.

length of this period was 4 h in March, 5 h in September and 4 h in December. The lower third of the middle transect would be covered during this time, and within this region salinities were lower as the river channel was approached. A rate of change of salinity of 28·5 ‰/h, was recorded during 1 h of this period in September.

In March, September and December, the surface water rapidly decreased in salinity around the time of high tide. At this time the surface water was covering that region of the middle transect which lies above MHWN, and within this region salinities were lower towards the upper end of the transect. The periods of exposure to this layer of less saline water were, March 5 h, September 3 h and in December approximately 6 h (3 h either side of high water). These surveys were carried out at spring tides; at neaps this less saline layer would affect a lower region of the transect.

THE HORIZONTAL DISTRIBUTION OF SALINITY

Horizontal salinity surveys were made once a month at high water of spring tides. High water had to be approximately 14 ft above ACD to allow the *R.V.* *PANDALUS II* to reach salinity station F at the head of the estuary. Tidal heights and dates of these surveys are shown in Table 2. It had been shown by the tidal cycle surveys that water movement would be at a minimum at high tide, and also that the salinity conditions would be more or less stable. The *PANDALUS* arrived at station A one hour before the calculated time of high water, moved slowly up the estuary and arrived at station F at high tide. The boat remained stationary above each salinity station while samples were taken with a Casella water sampler from the surface, 3 ft down, and from the bottom. The depth at which each bottom sample was taken was recorded with a lead line. Samples were titrated immediately so that they could be repeated if necessary.

Table 2. *Dates and tidal heights of horizontal surveys*

	Height of tide at HW (ft above ACD)		Height of tide at HW (ft above ACD)
7 Mar. 51	14·6	17 Sep. 51	14·7
6 Apr. 51	14·6	16 Oct. 51	14·3
21 May 51	14·8	29 Nov. 51	15·1
19 June 51	14·3	26 Dec. 51	13·7
19 July 51	14·6	28 Jan. 52	15·8
20 Aug. 51	14·5	25 Feb. 52	15·5

The tidal cycle surveys have shown that a tongue of less saline water extended over the surface of the estuary at high tide, but as the surveys were carried out at one place, they did not show how far the tongue extended down the estuary. To gain information on this point, one horizontal survey was carried out each month from 27 March 1951 to 25 February 1952 on suitable tides. The position of the isohalines shown in Fig. 5 were calculated from the three samples, surface, 3 ft and bottom, taken at each of six stations (A-F, Fig. 1). Vertical sections of the estuary were drawn on graph paper with the vertical scale (depth) much exaggerated, with horizontal lines for each sampling depth and vertical lines for each station. The eighteen salinity readings were inserted on the intersections of the resulting grid, and the point at which each isohaline crossed the grid lines was found by interpolation, assuming that salinity varied in proportion to distance between adjacent points of the grid. In Fig. 5 the lower transect is opposite station B, the middle transect is opposite station C, and the upper transect is opposite station E.

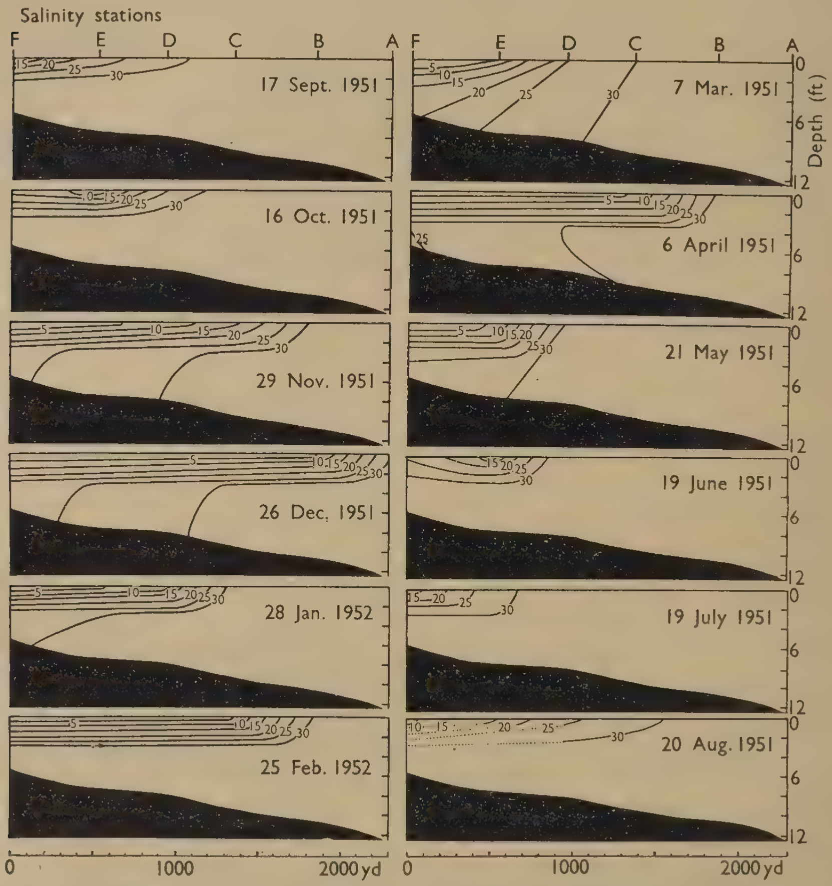

Fig. 5. The salinity of the estuarine water at HW of spring tides. Station E shows the conditions opposite the upper, station C opposite the middle, and station B opposite the lower transect.

It is evident that a well-marked salinity gradient was present at high tide throughout the year, and except for March when strong winds were encountered, the gradient is so marked that the isohalines were usually horizontal and close to the surface. If, for the purpose of this study, all water of greater salinity than

30 ‰ is regarded as sea water, the change from sea water to water of very low salinity, in most cases fresh water, takes place at most stations between a depth of 5 ft and the surface. As the surveys were commenced and completed at a definite period of the tidal cycle, and as the salinity of the bottom water entering the upper reaches was relatively stable at 33-34·5 ‰, the position and depth of the isohalines depended on the amount of river water entering from the head of the estuary before the time of high water. Seasonal variations in the rainfall of the River Blyth catchment area were suitably reflected by the surveys. The year investigated can be divided into the dry months of May to October, and the wet months of November to April, with May and November providing a transition between the two groups. Within the groups, August stands out as having had more, and January as having had less fresh water entering the estuary than would have been expected. The greatest amount of river water entered the estuary in December and the least in July.

SALINITY OF THE INTERSTITIAL WATER OF MUD

The effects of exposure on the interstitial water in the mud were studied along the three transects on three consecutive days in each month during June, September and December 1951 and March 1952 where this was possible. If it was not possible to do this in three days, the surveys were spread over four days. One transect was surveyed near the time of low water each day. In order that some comparison could be made between the salinity of the interstitial water and that of the tidal water, the three or four days selected followed one of the horizontal surveys already described. The horizontal surveys for June, September and December shown in Fig. 5 should therefore be consulted in relation to Figs. 6 and 7 (in Fig. 5 the drawing for March is not shown; it is identical with that for April 1951). The horizontal surveys were carried out on spring tides, usually the highest tide of the fortnightly series. The interstitial surveys were therefore on following tides, decreasing in height from the fortnightly maximum, but nevertheless the interstitial salinities would be near their maximum; they would be lower during neap tides when the ratio river : sea water would be at a maximum.

Considering the first series of recordings in Fig. 6, it will be seen that in general interstitial salinities were higher in June and September than in December and March. Comparison with the appropriate months in Fig. 5 will show that this was a reflection of the high tide salinities. The salinities of the first series were generally deflected downwards at each end of the transects during December and March, and to a lesser extent on the middle and upper transects during September and June. This confirms the observation made previously, that the periods of rapidly changing salinity of the tidal water at high and low water, affected respectively the upper and lower third of the middle transect. As they were completed the previous year, the actual values recorded during the tidal cycle surveys are not strictly applicable. Yet the general effect of the low salinities recorded over the lower third of the transects are seen in the interstitial salinities at the bottom end of the three transects in March and December, when there was more river water in the estuary. The effect of the less saline estuarine water on the interstitial water at the upper end of the transects was much more distinct. If the interstitial salinities for March are compared with the high tide salinities for April 1951 (identical with March 1951), salinities at the surface were 30‰ at the lower, 7‰ at the middle and <5‰ at the upper transect, while the corresponding first series of interstitial salinities at the upper end of the transects were 27‰, 16‰ and 16‰. A similar comparison could be made for December, although interstitial salinities at the upper end of the upper transect were higher than was expected; this may have been due to a decrease in the amount of river water in the estuary, perhaps caused by the period of intense cold at this time.

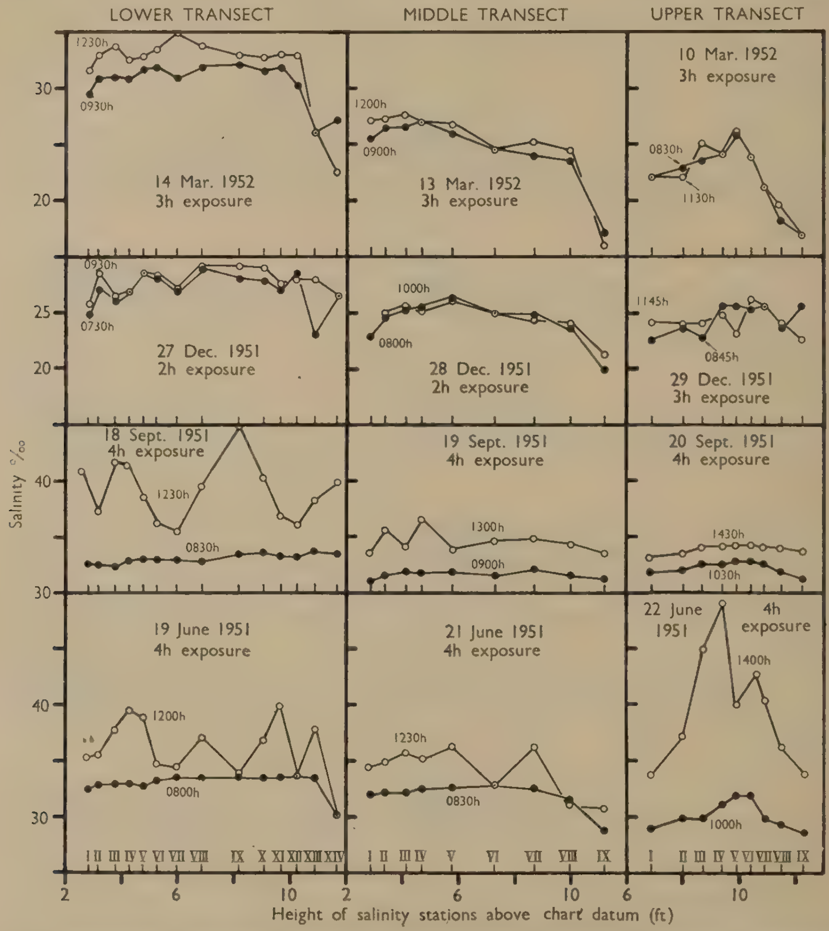

Fig. 6. Variations in the salinity of the interstitial water on the transects. First series ●-●-●, second series o-o-o, started at stated times.

Alexander *et al.* (1932, 1935) pointed out that interstitial salinities in the River Tees bottom deposits decreased steadily as samples were taken further from the sea. Table 3 presents average values for the first series of interstitial salinities over the whole transect, which are closest to those values left by the retreating tide. The same relation was generally found to hold, although the distances separating sampling points are much smaller in the Blyth than in the Tees, and differences between the lower transect and the other two were greatest during winter and spring when the influence of river water was greater. Even during these periods,

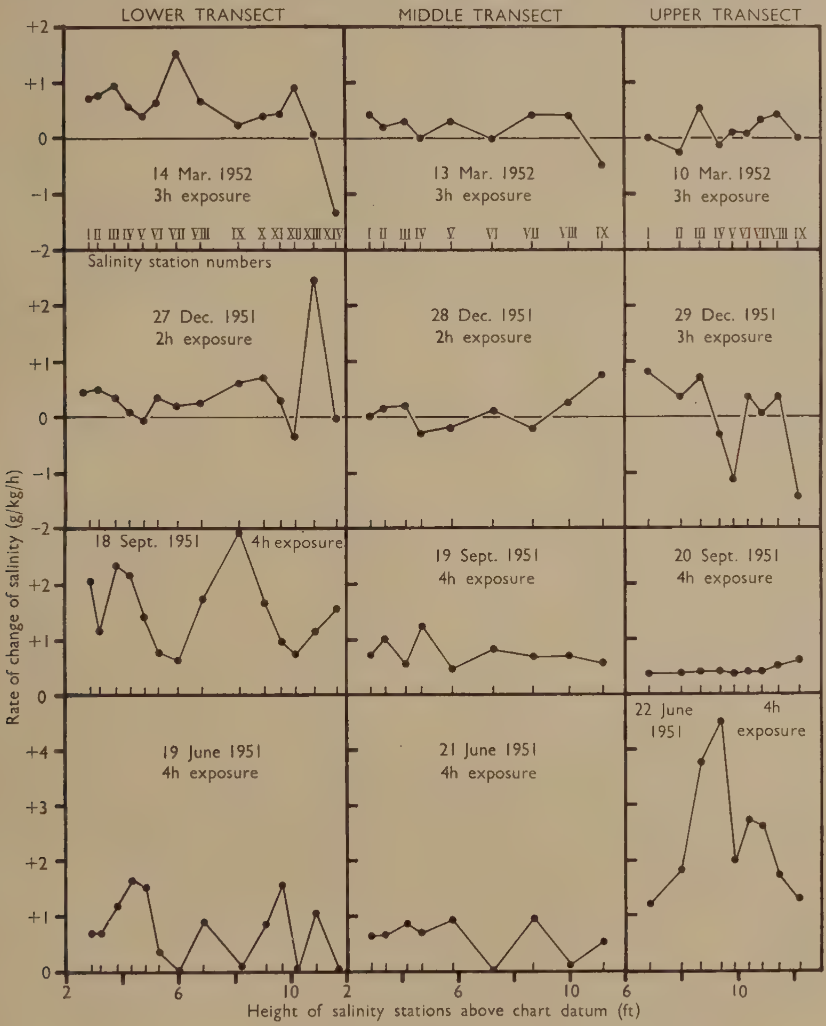

Fig. 7. Rates of salinity change of the interstitial water on the transects.

differences between the middle and upper transects were small by comparison with the Tees, and in some cases the average values for the upper transect were higher than those of the middle. There is little doubt that this was due to the fact that the sampling points on the former had been exposed, on the average, for longer periods before the first series of samples were taken, and exposure had consequently raised the salinity.

The effect of exposure to the air on the interstitial water is shown by the rates of change of salinity in Fig. 6. There are two ways in which salinity variations may be produced in the interstitial water of exposed mud. Firstly, fresh water may be added to the mud, either as drainage water from the fields surrounding the estuary or as rain (the latter did not occur during any of the twelve surveys); secondly water may be removed from the mud by evaporation. The effect of evaporation in June and September is shown by the considerable positive rates of change which were recorded on all transects. On the upper transect a rate of change of 4·5 ‰/h was recorded. This figure was exceptional, but had this rate of change continued for the whole time that the sampling point was exposed to the air (approximately 7 h), the change in salinity would have been 31·4 ‰. Generally the rate of change of salinity varied during June and September from 0 to +3 ‰/h.

Table 3. *Comparison of bottom water salinities at high water, and the average salinities of the first series of interstitial water surveys at low water*

	Lower transect		Middle transect		Upper transect	
	Bottom water	Interstitial water	Bottom water	Interstitial water	Bottom water	Interstitial water
June	33·75	32·95	34·0	31·9	33·3	30·2
September	33·9	33·1	33·7	31·6	33·0	32·2
December	32·4	27·0	32·2	24·1	27·6	24·3
March	32·2	30·5	30·7	24·5	27·4	22·0

In December and March positive rates of change were much smaller, only on one occasion exceeding 1·15 ‰/h. A number of negative changes were in fact recorded. As no rain fell during these surveys, the negative changes must be attributed to fresh water draining from the surrounding areas of arable land above the level of the transects, or from the gravel bed running between MHWN and MHWS which is in contact with water of reduced salinity at high tide. Drainage water would affect sampling points indiscriminately by following depressions and footprints made in the mud.

It is not possible to select any sampling point which had a consistently high or low rate of salinity change. This might imply that (1) salinities varied within each sampling point at the time when the first series of samples was taken, or that (2) the effects of exposure varied on the same transect during the same period of time, or that (3) some other factor, such as drainage water, was affecting salinities. The results shown in Fig. 6 for the middle transect in spring and winter, and the upper transect in autumn, show that (1) is unlikely, because, when the effect of evaporation is low, the first and second series readings are both similar and uniform. It is probable that this variation is a product of the combined action of (2) and (3), and that such factors as shelter from the wind and sunlight by stones, algae and variations in topography, and the indiscriminate effects of drainage water, were responsible. Attempts were made to correlate the effects of relative humidity and temperature with the rates of change of salinity. This was not possible in detail, although the broad differences between summer and winter were obvious. However, the effect of wind was not studied, and it is considered that this is one of the most important factors concerned in the evaporation of water from mud. Studies using evaporimeters at each sampling point would probably throw some light on the variable rates of evaporation from any particular sampling point, and provide valuable information on the sheltering effects of algae, stones and small depressions. It is well to point out here that one of the largest rates of change was recorded on the upper transect in June, when temperatures were below normal for the month, relative humidity was above normal, but there was a strong north-west wind.

On 28 March 1951 the effect of low salinity channel water on the interstitial water of nearby mud was investigated. The falling tide was followed down the upper transect until the river channel attained a constant level. Samples of mud were taken within 6 in. of the river edge, together with water samples from the river itself every hour for 5 h. On all six occasions the river water had salinities of less than 1‰, while the salinity of the interstitial water was 21·8‰, 21·4‰, 21·7‰, 22·2‰, 23·2‰ and 23·5‰. The salinity of the interstitial water remained considerably higher than that of the river water, and furthermore it became more saline with exposure.

As salinity stations B, C and E are opposite the lower, middle and upper transects, it is possible to compare the salinity of the bottom water at high tide with the average of the first series of interstitial salinities at low tide. Table 3 shows that bottom water salinities are higher in every case (cf. Alexander *et al.* 1935) even though, because of the effects of exposure, the interstitial salinities were probably higher than those left by the retreating tide.

DISCUSSION

Using the tidal cycle and the horizontal surveys, it is possible to reconstruct the general salinity changes occurring during a spring tidal cycle. These provide the general principles behind the salinity characteristics of the estuary, and the effect of other factors will modify this pattern to varying degrees.

As the tide rises, the sea water entering the middle and upper reaches mixes thoroughly with the river water travelling in the opposite direction. The sea water advances at maximum speed at half tide, and it is at this time that it probably exerts its greatest damming effect on the river water. As high tide is approached and the tide advances less rapidly, the river water intrudes over it as a layer. Stratification is then established, and mixing takes place mainly in a vertical direction. As the tide recedes the layer of less saline water on the surface is both lowered vertically and carried towards the sea. During this period it is constantly being reinforced from the river. At those points in the estuary where the less saline surface layers approach the bottom, mixing with the more saline layers takes place.

Four factors may affect this overall pattern to varying extents: tidal range and heights, the rate of flow of the river, wind and rain. In general, salinities will be lower during neap tides because less sea water enters the estuary. At neaps the initial rise of the tide starts nearer the head of the estuary, and the rate of advance of the rising water is reduced. Less thorough mixing with the river water ensues, and the damming effect is less acute. The tongue of fresh water will form earlier than during spring tides at a position nearer the mouth of the estuary, and as a result of the reduced height of the tide it will lie at a lower vertical height. As the tide recedes the layer of less saline water will approach the bottom deposits at a lower level than during springs, and the salinity variations produced as a result of mixing with the bottom water, will affect different areas of mud.

The effect of seasonal variations in river flow is superimposed on the tidal cycles. When the rate of flow is larger, salinities in the advancing front of sea water will be lower during the flood tide, and as the damming effect of the opposing bodies of water is larger, vertical stratification by the tongue of fresh water will probably be established at a point earlier in the tidal cycle. The tongue of fresh water will be thicker, salinities at the surface will be lower, and it will extend further down the estuary at high tide. When the rate of flow of the river is smaller, the other extremes of these effects will operate. The strong winds encountered during the horizontal survey of March 1951 disturbed the stratification normally established at high tide, but did not destroy it altogether. The velocity and direction of the wind are obviously important, as they determine the extent to which stratification is altered. Heavy rain was not met with during any of the surveys, and it is therefore difficult to assess its direct effect on the salinity of the tidal water. However, it is felt that precipitation must be very heavy to exert any appreciable effect.

Seasonal variations in the salinity of the tidal water produce corresponding variations in the interstitial water of the mud. The average values for the first series of interstitial salinities on the transects in Table 3 show that the lowest average interstitial salinities occurred in December and the highest in September; the maximum seasonal variation was 10·2 ‰ and the minimum was 6·1 ‰. The rapid and extreme variations shown during some of the tidal cycles do not appear to have produced corresponding short-term variations in the interstitial water over the whole length of the transects. The deflection of the interstitial salinities at the upper end of the transects is probably caused by the combined action of the less saline surface layer at high tide and the fresh water draining from above the transects at low tide. On the other hand, deflections at the lower end of the transect can only have been caused by the lowering of tidal water salinities near low tide. Nicol (1935 p. 235) has pointed out that, in a salt marsh 'the salinity of the surface inch of mud follows that of the [overlying] water fairly closely, but shows a considerable lag in reaching its maximum and minimum values, and seldom reached the same extremes of salinity'. The overlying water in the salt marsh pools showed much slower rates of change than those occurring in the tidal water in the estuary, but there is little doubt that diurnal variations in salinity are reflected in the interstitial water at the upper and lower ends of the transects. These effects are probably more extreme during neap tides when the river is in spate, and the less saline surface layer influences points further from the top of the transects.

Well-marked seasonal variations in the effect of exposure on interstitial salinities have been demonstrated. Alexander *et al.* (1935) found no appreciable change in the salinity of interstitial water in the Tees while it was uncovered during the ebb tide, but changes of up 1·15 ‰/h were recorded in the Blyth during December and March, and up to 4·5 ‰/h in June and September. In the latter two months the salinity of the interstitial water was raised well above that of sea water to 49·1 ‰ during the short periods of exposure that were studied. During the full period of exposure, these were presumably raised even higher, being slowly reduced when the mud was once again covered by the tidal water. Thus the interstitial water is subject to three distinct types of variation: short-term variations produced by exposure, short-term variations produced by tidal water at high tide and just before low tide, and long-term variations produced by fortnightly and seasonal variations in the salinity of the tidal water.

Little work has been done on the salinity tolerance of animals to salt concentrations greater than that of sea water, or of animals living in estuaries more saline than the sea (Day 1951). In view of the results presented in this paper, there is clearly a need for experiments in this field. However, it must be borne in mind that Nicol (1935) and Reid (1930, 1932) have shown salinity variations to be less extreme with increasing depth in the mud or sand, and pointed out that in considering the distribution of estuarine animals the normal depth in the substratum at which the animal lives is of great importance.

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SUMMARY

1. The River Blyth estuary is 3·8 miles long; the middle and upper reaches are almost emptied of tidal water at LWS, exposing extensive areas of intertidal mud.

2. High tide salinities in the middle and upper reaches were determined on one spring tide in each month for 12 months, and the salinity variations during the twelve-hour cycle were examined at one place in the upper reaches every 3 months during a period of one year.

3. A simple method for extracting interstitial water from mud is described.

4. Well-marked vertical stratification was established at high tide, when a surface layer of reduced salinity spread down the estuary. The extent of this layer, and salinities at the surface were determined by the rate of entry of fresh water from the river.

5. Interstitial salinities were found to reflect the seasonal salinity variations of the tidal water.

6. Salinity variations in the tidal water during a twelve-hour cycle caused but little variation of interstitial salinities, only affecting the upper and lower ends of the transects in certain months.

7. The seasonal effects of exposure on the salinity of the interstitial water is described for three transects in the upper reaches of the estuary. In June and September positive rates of change of up to 4·5 ‰/h were recorded, while in January and March positive rates of change rarely exceeded 1·15 ‰/h, and a number of negative changes were recorded. Some inconsistencies are noted, and the probable explanation is discussed.

8. Exposure has been found to cause rapid positive rates of change in the salinity of the interstitial water during the summer months. On these occasions the mud-dwelling animals living within 2 cm of the surface would have to withstand salinities almost twice that of sea water.

9. The general pattern of salinity variations during a tidal cycle is reconstructed, and the factors affecting this pattern are discussed.

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THE EPHEMEROPTERA OF A STONY STREAM

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(With 5 Figures in the Text)

This is first an account of the population of Ephemeroptera in a small stony stream of the type to be found anywhere among hills of impervious rock. Secondly, comparison is made between this and other similar streams in the Lake District and in other parts of Europe. This leads to a comparison with stony rivers, and then there is a discussion, more general because there is less information, about the species typical of slow-flowing and stagnant waters. Finally the various species found are taken one by one and their habitats described.

A species list is the starting point, but no more than that, and proper comparisons must be based on the number of each of the various species present. As soon as numbers have to be studied, a crop of problems is encountered. First there is the question of sampling. This has been discussed elsewhere (Macan, in press) and here only a brief account of methods is given. When reasonably comparable catches are possible, there are several points intrinsic to the animals that need study. The life history must be known, so that catches at different places are made at a time of year when the species is abundant; as will be seen, some spend a surprisingly long time dormant in some stage that is missed by ordinary collecting methods. The numbers at any given time will not be the same this year in any particular place as they were last year and next year again the total will be different; the work was carried on for three years to gain some idea of this variation. Then in any one year at any given time the population will not be uniform throughout the length and breadth of the beck. Accordingly, after an account of the stream and the methods, these various fluctuations and differences are examined. Afterwards the comparisons are made.

THE STREAM

(a) *Topography*

Ford Wood Beck may be described as a moorland stream, though most of the drainage area is cultivated. Its chief feature is that, except at the extreme top of one of the tributaries, it has a stony bed on account of the swiftness of the current. It is quite small, nowhere more than 2 m wide and generally not much over ankle-depth, except after rain when it runs at knee-depth or more. Moss grows on exposed rock and a few of the largest stones but not elsewhere, and from this it is judged that the bottom is unstable. After a flood there is sometimes a bank of stones where there was no bank before, but widespread disturbance of the substratum has not been seen, nor reduction in the fauna after a flood noticed. Much of the course is artificial and the farmers rake the stones out when they accumulate in banks.

Very roughly the beck has the form of a trident, with the outer arms divergent (Fig. 1). The shaft of the trident lies in a valley that was deepened or excavated by the ice, which left behind two basins, for there is an outcrop of rock just below the 'k' of 'Ford Wood Beck' in Fig. 1. The lower holds Blelham Tarn, the upper is filled with material brought down by the ice or washed in soon after the ice retreated.

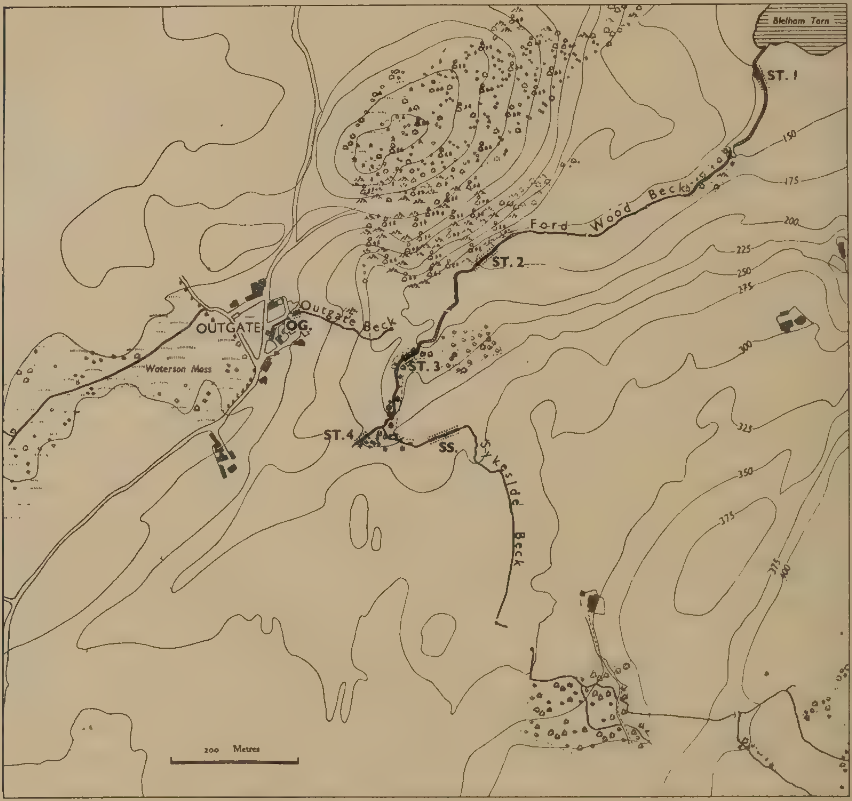
Blelham Tarn
ST. 1
150
175
200
225
250
275
300
325
350
375
375
400
Ford Wood Beck
ST. 2
Outgate Beck
OUTGATE
OG.
ST. 3
Waterson Moss
ST. 4
SS.
Sykeside Beck
200 Metres

Fig. 1. Ford Wood Beck and its tributaries; altitudes in feet.

Near the head of this rather flat valley (fall about 1 in 56), the beck receives its two main tributaries, the outer arms of the trident, and a little higher up all three flow down the steep sides of the valley (fall about 1 in 12·5). At the top of the sides of the valley there is a plateau (Fig. 2) across which the two tributaries run, though the main stream flows underground in an artificial culvert. The tributary known as Outgate Beck rises on the plateau in a bog, but the other, Sykeside Beck, flows across it to rise on a steep slope just off Fig. 1. This part of the system was not investigated.

The position of the six stations is shown in Figs. 1 and 2. Station 1 was close to the mouth in a stretch with fair flow and a bottom with stones of all sizes owing to the proximity of the rocky outcrop. The largest a man could scarcely lift with one hand. They were all comparatively flat and beneath them there were smaller stones overlying gravel and sand.

The region shown narrow on Figs. 1 and 2 is deep with sheer banks and with small stones only on the bottom, presumably because the current has never been strong enough to wash larger stones so far down the valley. *Sparganium ramosum* Huds. subsp. *neglectum* (Beeby) Schinz & Thell. grows in this reach, which is protected from the full force of a flood because the water flows out on to the field and re-enters the channel lower down. The only other higher plant is *Mimulus luteus* L. which grows near station OG, where it has probably been planted. At station 2 the flow is also relatively slow, but stones vary more than might be expected in size, because rejects from a wall have been thrown into the stream here.

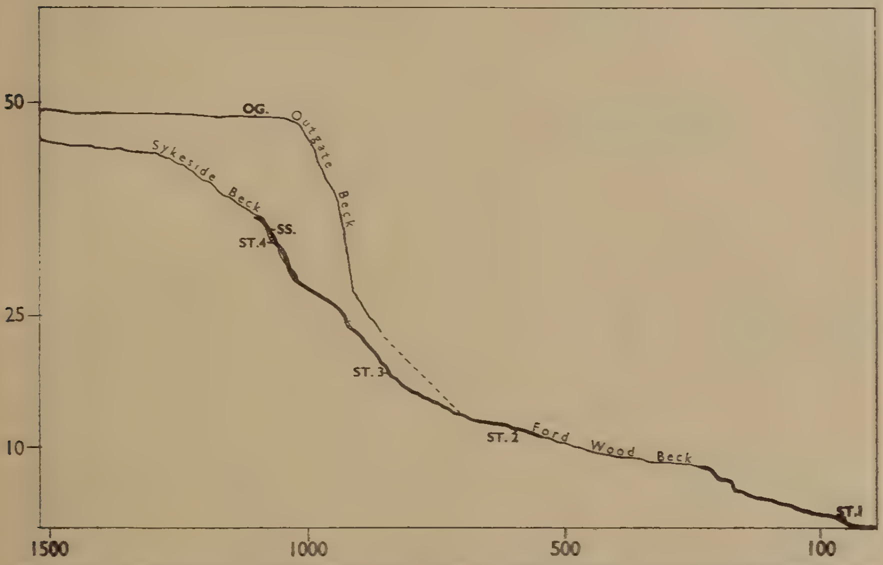

Fig. 2. Ford Wood Beck and its tributaries in profile; scales in metres. The horizontal scale starts from the mouth of the stream, which is just beyond the margin of the figure. The vertical scale starts from the base line.

Station 3 lies at the foot of the steep part of the stream and has a torrential facies, cascades alternating with pools full of stones and boulders. The station lies in a gorge, because the stream flows through a mound of boulder clay at this point and has had sufficient volume and force to cut down to the rock beneath. Above station 3 there are extensive stretches of bare rock. At station 4 the slope is still steep, but the boulder clay has not been eroded because there is less water even after heavy rain, most of which must seep through the ground to reach the stream.

At SS, the station in Sykeside Beck, the slope is gentler and the stream has not eroded down to rock although more boulder clay has been removed than at station 4. The stones left behind after finer particles have been swept away are more rounded than elsewhere in the stream, owing to abrasion while they were being moved by the ice. They are of all sizes and the largest is bigger than a man's head.

Station OG in Outgate Beck, is in an artificial walled channel in the writer's garden; flow is relatively slight and the stones small to medium-sized. A few hundred metres farther up, the beck originates in a moss in what was probably once a shallow lake basin. It flows through the moss in an artificial cut that is almost stagnant and heavily overgrown with *Potamogeton natans* L. and *Callitriche* sp. except for a month or two after the farmer has cleaned it out, which he does about once a year.

Outgate Beck has not been known to dry up in 20 years, though the water gets very low sometimes. Sykeside Beck does dry up in a fine summer. Mr W. Palmer, who owns it, tells me that the main beck above station 4 has not dried up in the last 50 years.

(*b*) *Climate*

A recording thermometer was installed at Outgate late in 1950, and a full discussion of results obtained with it will, it is hoped, be published elsewhere. The temperature sometimes reaches 0° C in winter but is generally a few degrees above it and the water never freezes. In April, May and June, temperature rises, and the diurnal fluctuation may be as much as 6° C. Later the fluctuation is less, and in the autumn the temperature sinks slowly with usually only a small difference between night and day. The temperature is generally between 16 and 17° C at the maximum in hot weather and the highest recorded was 19° C. A maximum and minimum thermometer at station 1 revealed a larger fluctuation in any given period with a maximum of 21·5° C. Station 4, on the other hand, as would be expected, had a more uniform temperature.

The year 1949 had an exceptionally long and fine summer. The following three, the years when the collections were made, were all rather similar with least rain in early summer and a fair amount during the rest of the year. In 1952 there was a dry spell in May longer than any dry spell in either of the other two but a fair amount of rain in June. There was another dry period in November. The first half of 1951 was notably colder than that of the other two years.

(*c*) *Flow*

Measurements of the surface flow were (cm/sec):

Station	1	1 (runnel)	2	3	OG
Timed float	49	87	45	38	40
Current meter	65	–	35,40,60	60-120	–

METHODS

Station 4 was not established till April 1951. Collections from the other five stations were made once a month in 1951 and 1952, but not as regularly in 1950 as the importance of a sample every month had not been realized then.

Collecting took a week, one station being visited early each morning so that the rest of the day could be spent sorting and the animals picked out before they died.

Regular collections and collections from many different places demand a method that can be operated in a flood or in a drought, and among large stones or small. The only instrument fulfilling these conditions seems to be a coarse-meshed net The one used had a circular mouth 26·5 cm across and holes about 1 mm square (20 threads to the inch). Collecting lasted exactly ten minutes, during which time the collector walked upstream lifting stones and holding the net in such a way that anything dislodged was swept into it. The stone was sluiced to and fro in the mouth of the net until all organisms visible to the naked eye had let go. A station (Fig. 1) consisted of a stretch of beck in which conditions appeared to be uniform about 50 m long. Collecting generally extended over a few metres only. The uppermost part of each station was visited only occasionally to make certain that the collecting and disturbance of the bottom in parts visited more often was not reducing the fauna.

From October 1951 onwards additional five-minute collections were made with a net of material used for collecting phytoplankton, and this caught enormous numbers of tiny nymphs that passed through the coarse net. From August 1952 to May 1953 collections were made with a shovel sampler.

SAMPLE VARIATION

Before the results of the collections are discussed, some information about the difference between two collections which, as far as possible are exactly comparable, is useful. It was obtained by collecting with the coarse net for two periods of five minutes instead of for one period of ten minutes, in other words doing the collection in two halves, and this became a standard practice after March 1952. The numbers of four species caught in the two halves are shown in Table 1 and, when the sum of the two totals exceeds 12, the ratio of the smaller to the larger is given. This is not a very satisfactory comparison from a statistical point of view but it is a simple and useful rough one. These ratios are grouped in Table 2. In 50% of the collections of three of the species, and more than that of *Rhithrogena*, the larger was less than half as big again as the smaller. In up to 16·6% of collections the ratio was over 1 : 2·5. The biggest anomalies were *Rhithrogena* 3 and 36 at station OG in October, *Ecdyonurus* 87 and 22 at station 2 in September and *Baëtis rhodani* 6 and 46 at station 3 in June and 16 and 66 at SS in August. There is little more that can be done with these figures. They indicate that the species are not evenly distributed over the stream bed but what the aggregation of any species may be due to is not known. They make it clear that a single collection can give a highly misleading idea of the numbers in a given stretch of stream.

Table 1. *Comparison of two halves of the coarse net collections (1952)*

The figures show the numbers of each species caught, and where the total exceeds 12 the ratio of the larger to the smaller catch (in parenthesis).

	Stations										
	1		2		3		SS		OG		Totals
Rhithrogena semicolorata											
Mar.	– –		52 39	(1·3)	100 81	(1·2)	3 10	(3·3)	– –		155 130
Apr.	56 38	(1·5)	82 69	(1·2)	26 15	(1·7)	– –		23 24	(1·0)	187 146
June	4 6		8 7	(1·1)	0 5		0 4		6 3		18 25
Sept.	2 1		4 5		10 15	(1·5)	2 1		7 4		25 26
Oct.	17 38	(2·2)	36 28	(1·3)	59 43	(1·4)	7 22	(3·1)	3 36	(12·0)	122 167
Nov.	104 78	(1·3)	98 127	(1·3)	143 253	(1·8)	21 27	(1·3)	35 83	(2·4)	401 568
Dec.	70 94	(1·3)	74 90	(1·2)	40 57	(1·4)	22 20	(1·1)	48 54	(1·1)	254 315
Ecdyonurus torrentis											
Mar.	– –		0 4		8 1		7 1		– –		15 6
Apr.	12 14	(1·2)	17 4	(4·2)	1 1		– –		5 2		35 21
June	6 7	(1·2)	20 9	(2·2)	1 0		0 0		1 7		28 23
Sept.	7 15	(2·1)	87 22	(4·0)	36 34	(1·1)	20 7	(2·9)	40 32	(1·3)	190 110
Oct.	7 9	(1·3)	36 27	(1·3)	17 38	(2·2)	5 9	(1·8)	14 17	(1·2)	79 100
Nov.	26 20	(1·3)	82 40	(2·1)	52 83	(1·6)	23 7	(3·3)	29 32	(1·1)	212 182
Dec.	8 19	(2·4)	20 19	(1·1)	14 13	(1·1)	10 4	(2·5)	11 8	(1·4)	63 63
Baëtis rhodani											
Mar.	– –		187 87	(2·1)	122 151	(1·2)	30 32	(1·1)	– –		339 270
Apr.	60 136	(2·3)	73 63	(1·2)	41 45	(1·1)	– –		74 72	(1·0)	248 316
June	67 90	(1·3)	104 47	(2·2)	6 46	(7·7)	102 40	(2·6)	43 20	(2·2)	322 243
Aug.	95 73	(1·3)	42 125	(3·0)	163 72	(2·3)	16 66	(4·1)	23 17	(1·3)	339 353
Sept.	114 159	(1·4)	150 135	(1·1)	82 64	(1·3)	79 137	(1·7)	3 16	(5·3)	428 511
Oct.	38 67	(1·8)	44 84	(1·9)	38 84	(2·2)	49 33	(1·5)	3 1		172 269

Nov.	77	(1·1)	33	(1·9)	62	(2·6)	61	(1·1)	30	(1·4)	263
	85		64		164		66		21		400
Dec.	70	(1·3)	40	(1·1)	10	(1·4)	21	(1·6)	13	(2·2)	154
	56		36		7		13		6		118
Baëtis pumilus											
Mar.	–		1		20	(1·4)	2		–		23
	–		10		14		2		–		26
Apr.	15	(3·1)	9	(2·4)	19	(1·6)	–		8	(1·5)	51
	46		22		30		–		12		110
June	14	(1·5)	12	(1·0)	12	(1·6)	18	(1·1)	38	(2·0)	94
	21		12		19		16		19		87
Aug.	5		1		9	(1·3)	2		19	(1·2)	36
	5		2		7		10		22		46
Sept.	8	(2·5)	4		1		7		47	(1·6)	67
	20		2		7		4		29		62
Oct.	0		3		3		0		2		8
	5		1		0		0		3		9
Nov.	7	(1·0)	3		5		2		4		21
	7		5		6		2		8		28
Dec.	1		0		0		1		2		4
	7		0		0		0		0		7

Finally, can these figures be converted to number per unit area? Specimens of *Baëtis* up to 5 mm long can pass through the coarse net and do so in a proportion that increases with decreasing size. Moreover, the shovel sampler does not sample the population properly because it disturbs nymphs before they are right inside it and they swim away. Therefore the numbers of *Baëtis* per unit area cannot be assessed. The flat nymphs are more satisfactory in this respect. Nymphs of *Rhithrogena* have to be under 3 mm long before they pass through the coarse net and there is no evidence of any error in the shovel sample. This does contain a significantly higher proportion of tiny nymphs when its catch is compared with one made with a fine net, probably because the smallest nymphs inhabit the gravel and smaller stones, which are passed over during the course of a net collection. However, if months in which there are many specimens less than 3 mm long are omitted, the catches made with the net can be converted to numbers per unit area. As the result of an analysis made elsewhere (Macan, in press) it was concluded that in five minutes a net catches a little more than twice as much as a shovel sampler sampling 0·05 sq. m. For the sake of convenience it may be treated as exactly twice as much; there is no point in being too exact with figures obviously subject to a large error. Therefore the figures in Table 1, if the catches in September and October are omitted, represent the population of nymphs in 0·1 sq. m. In March and April, the average number of *Rhithrogena semicolorata* at stations 1, 2 and 3 is 58 with a standard deviation of ±27. In November and December the average is 102 with a standard deviation of ±55. No net collections were made after this but shovel samples were taken at station 2, and they are worth quoting for the sake of comparison. In the first five months of

Table 2. *Ratios of the two halves of the coarse net collections*

The figures give the numbers of collections for which the ratios fell between the limits indicated.

	1 : 1-1·5	1 : 1·6-2·0	1 : 2·1-2·5	1 : over 2·5	Total
Rhithrogena	17	2	2	3	24
Ecdyonurus	12	2	6	4	24
Baëtis rhodani	18	5	7	6	36
B. pumilus	8	4	2	1	15

1953, there were on the average 70 *Rhithrogena semicolorata* in 0·1 sq. m and the standard deviation was ±30. When shovel sampler and fine net collections of *Ecdyonurus* are compared, there is little difference in the proportion of any size-group, and therefore all the net collections may be translated into numbers per unit area in this way. The same is probably true of the other species, though allowance must be made for escape through the net of tiny nymphs of forms such as *Paraleptophlebia.*

THE SPECIES FOUND

Table 3 includes all the species ever caught and gives the totals for 1951. It need hardly be pointed out that totals of this kind must be analysed before their precise significance can be evaluated, but for the moment they are useful because they help to divide the species into three categories. The first four species were abundant and rarely absent from any catch made at an appropriate time of year; it may be deduced that they are the species whose optimum habitat is provided by a stream of the kind studied. *Ephemerella ignita* is a borderline case, its low total being due partly to a very short season and to the fact that it is confined to the lowest reaches of the stream. The next five species were taken fairly regularly, though rarely or never in large numbers; presumably their optimum habitat is not provided by Ford Wood Beck; the numbers of the last two are so small that they have been ignored in the pages that follow. Finally come three casuals, the last two of which had probably been washed down from quieter reaches higher up.

Table 3. *Total numbers of Ephemeroptera caught in coarse net collections at five stations in 1951*

Very small nymphs of *Ecdyonurus* that could not be named with certainty have all been assigned to *E. torrentis.*

Baëtis rhodani (Pictet)	3044	*Paraleptophlebia submarginata* (Stephens)	127
Rhithrogena semicolorata (Curtis)	2990	*Habrophlebia fusca* (Curtis)	26
Ecdyonurus torrentis Kimmins	1336	*Ecdyonurus venosus* (Fabricius)	26
Baëtis pumilus Burmeister	628	*Baëtis scambus* Eaton	1
Heptagenia lateralis (Curtis)	223	*Siphlonurus lacustris* Eaton	1
Ephemerella ignita (Poda)	113	*Cloëon dipterum* (Linnaeus)	1

That is the fauna of the beck as revealed by collections at the stations regularly visited but a complete list includes also *Leptophlebia vespertina* (Linnaeus) and

Centroptilum luteolum (Müller). *Leptophlebia* was found in 1947 in the moss in which Outgate Beck rises but not subsequently; *Cloëon dipterum* was abundant there in 1949 and scarce in 1951, and no Ephemeroptera at all were taken in 1950 though three visits were made. Probably these still-water species are washed away when the vegetation is removed and the regular cleaning of the cut prevents either establishing itself. *Centroptilum luteolum* was found several times in the slowest

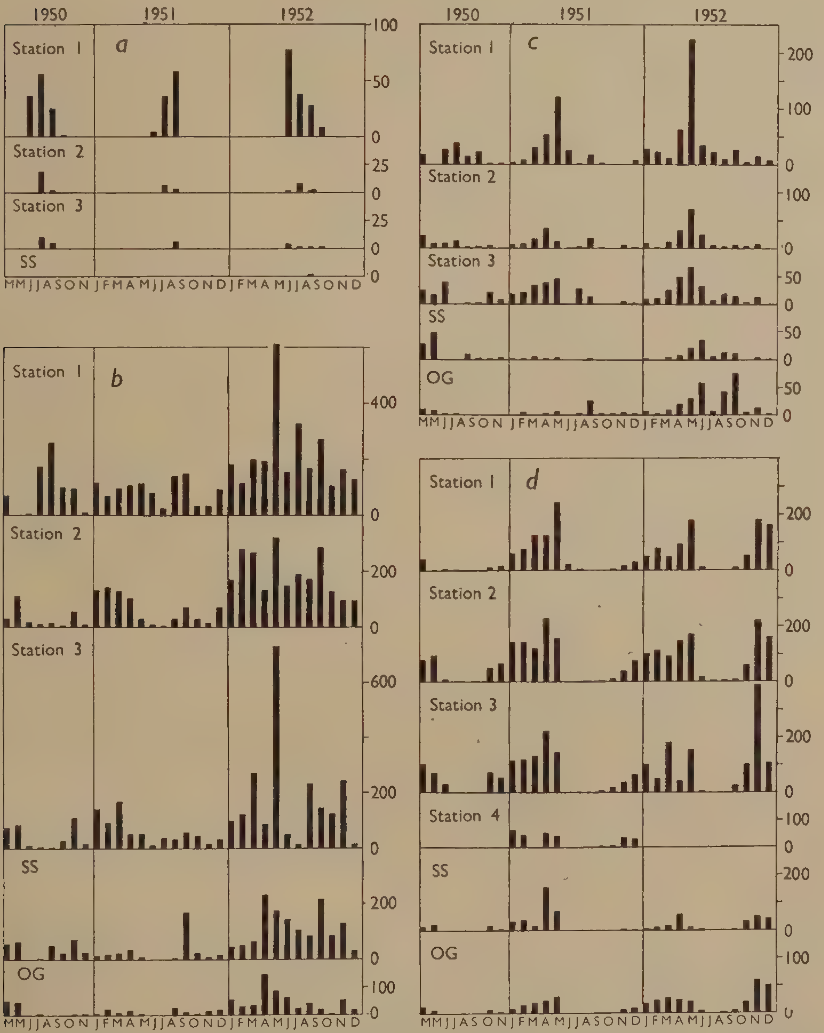

Fig. 3. Numbers of: *a*, *Ephemerella ignita*, *b*, *Baëtis rhodani*, *c*, *B. pumilus* and *d*, *Rhithrogena semicolorata* caught at each station each month.

part of the main beck where the *Sparganium* grew. *Siphlonurus* was found in 1955 in a short ditch fed by a field drain, a relatively stagnant backwater overgrown with *Callitriche* sp. The place had not been visited before and *Siphlonurus* may well occur in it regularly.

LIFE HISTORIES

The life histories have been described elsewhere and the purpose of considering them here is to discover at what times of year each species is numerous in order that fair comparison of the various catches with each other and with published records may be made. Numbers caught in each month of the three years, set out separately for each station, are given in Figs. 3 and 4. *Ephemerella ignita* is a summer species found in June, July and August, scarce in September and absent in all the other months when it is thought to be in the egg stage. *Baëtis rhodani* and *B. pumilus* can be found in every month. Eggs hatch in the autumn and winter and give rise to a generation that is adult from spring to August. The progeny of

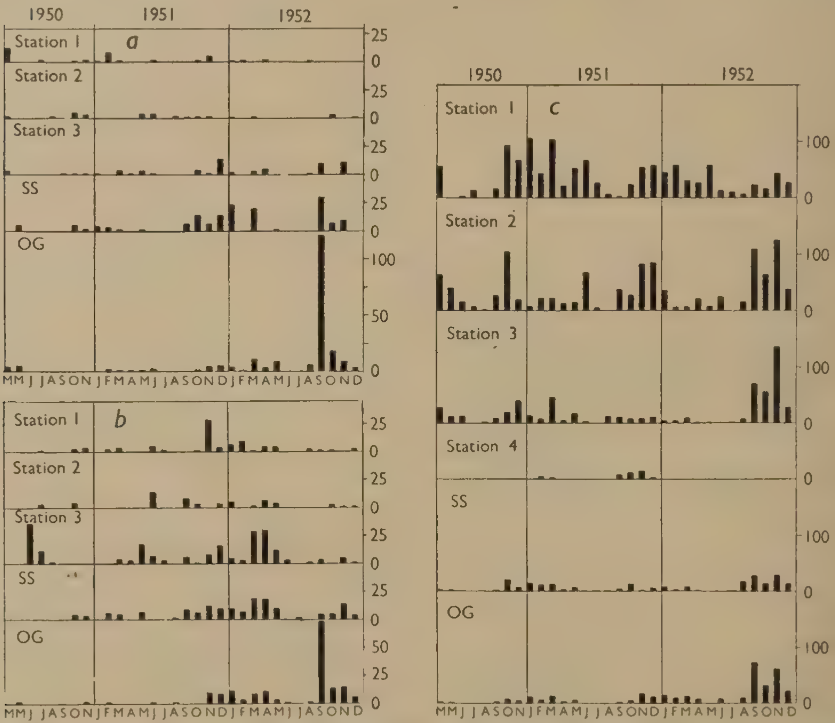

Fig. 4. Numbers of: *a*, *Paraleptophlebia submarginata*, *b*, *Heptagenia lateralis*, *c*, *Ecdyonurus torrentis* caught at each station each month.

these specimens complete development within the season and are on the wing from August to November. The rest, like *E. ignita*, have one generation a year, but, in contrast to that species, are present all winter and scarce or absent in summer.

These figures show clearly that two collections a year are imperative for a reliable picture of the fauna; one in July or August for *Ephemerella* and one in winter for the others. It follows that conclusions based on a summer vacation study would be misleading. All the winter species appear in autumn but two of them, *Rhithrogena semicolorata* and *Baëtis pumilus*, continue to become more numerous in each successive month right up to the time when numbers fall on account of emergence. Strictly, then, the catch in one month is not comparable with that in any other month. In *Baëtis pumilus*, the increase is so great that this source of error cannot be ignored. In *Rhithrogena* the increase is much less after January, and since the numbers were not obtained by a particularly accurate method in the first place, no serious error will arise if catches made in any of the five months January to May are treated as exactly comparable.

FLUCTUATIONS IN POPULATION

Ephemerella ignita completes a cycle within a calendar year. Both species of *Baëtis* have two generations a year, but the end of one and the start of the next overlap and there is no gap to provide an obligatory point from which to begin summing the total. It may therefore be conveniently presented per calendar year also and this is done in Table 4. In 1950, collections were made only in March and May to November, and a comparison of the three years can be based on the catches in these months only; totals for twelve months in 1951 and 1952 are also shown. For the remaining species, which have one generation that grows through the winter, totals must be per season not per annum; August has been taken as a convenient starting point (Table 5). The period of survey included only two seasons but it is possible to compare all three years for the months August to November inclusive. Totals for August to December inclusive in 1951 and 1952 are also shown.

Table 4. *Annual totals of* Ephemerella *and* Baëtis

The totals for *Baëtis* include the months of March and May to November only. Twelve-month totals for 1951 and 1952 are shown in parentheses.

	1950	1951	1952
Ephemerella ignita	152	113	172
Baëtis rhodani	1712	1620 (3044)	6103 (8919)
B. pumilus	405	309 (628)	770 (1273)

Every one of the seven species was most abundant in 1952. All but the two least numerous, *Paraleptophlebia* and *Heptagenia*, were more abundant in 1950 than in 1951, though only slightly so. There is no obvious explanation of this. In 1952 rainfall was somewhat more evenly spread than in the other two years and the early summer drought was confined to May, but otherwise the year had no outstanding climatic peculiarities. Ten times as many *Rhithrogena* were taken in 1952 as in 1951 (Table 5) but these figures are not based on a full season and the comparison is not a fair one. The high total of *Paraleptophlebia* in 1952 was largely due to one catch of exceptional size (Fig. 4). *Heptagenia lateralis* was seven times more numerous in 1952 than in 1950 but again the comparison is not based on a full season. *Baëtis rhodani* was about three times more abundant in 1952 than in 1951. These fluctuations are not particularly large and the general impression is of a stable population, which is to be expected, because the stream appears to provide a stable environment.

Since some species move up or down stream during the year, simple totals over a period do not make it possible to compare the populations at different stations reliably. Nevertheless, Figs. 3 and 4 give a clear impression. *Ephemerella ignita* abounds only at station 1 and is scarce or absent farther up. All the rest occur at all the stations fairly regularly. Numbers of the four more numerous species, *Baëtis rhodani*, *B. pumilus*, *Rhithrogena semicolorata* and *Ecdyonurus torrentis*, are distinctly higher at the three lowermost stations; those of the two less numerous species, *Paraleptophlebia submarginata* and *Heptagenia lateralis*, rather higher in the upper parts of the stream.

Table 5. *Annual totals in the seasons 1950-51 and 1951-52 omitting December, and in the years 1950, 1951 and 1952 for the months from August to November inclusive*

Totals for August to December inclusive in 1951 and 1952 are shown in parentheses.

	1950-51	1951-52	Aug. – Nov.		
			1950	1951	1952
Rhithrogena semicolorata	2968	2098	307	133 (329)	1308 (1887)
Ecdyonurus torrentis	1195	1207	446	407 (587)	933 (1062)
Paraleptophlebia submarginata	70	171	23	47 (80)	227 (232)
Heptagenia lateralis	100	372	20	97 (139)	148 (160)

The numbers of *Baëtis rhodani* at stations 1, 2 and 3 are close in all three years, though always highest at station 1, which may be due to a downstream migration, for there is always some period in summer when an unusually high proportion is found there. *B. pumilus* is similar. In its two complete seasons, *Ecdyonurus torrentis* was most abundant at station 1, though twice in the autumn its biggest population was higher up. *Rhithrogena semicolorata*, on the other hand, is most abundant at stations 2 and 3. *Paraleptophlebia submarginata* is the only species with a tendency to be most abundant in the two tributaries, Sykeside and Outgate. *Heptagenia lateralis* is not dissimilar, though in both complete seasons its greatest numbers were at station 3.

The analysis just made has shown that the catches in the months January to May inclusive, though not strictly, are roughly comparable, and that in this period stations 1, 2 and 3 have similar, though not identical populations, if *Ephemerella ignita* be excluded. From this period and these places it is therefore possible to derive a general picture with which individual collections may be compared. There are then five months and three stations, thirty collections altogether in the two years 1951 and 1952 (Figs. 3 and 4). If the two halves of one collection be treated separately (Table 1), there are twenty collections in 1952 and therefore thirty-five in all. First presence or absence may be considered. The four common species were taken in every ten-minute catch and there was only one absence in a five-minute catch—*Ecdyonurus torrentis* (Table 1). *Paraleptophlebia submarginata* was not taken in seven of the fifteen stations in 1951 and ten out of the twenty in 1952; in one month, May 1952, it was absent from all three stations. In both years it was a more constant member of the fauna of Sykeside and Outgate Becks and in no month was it absent from both (Fig. 4). *Heptagenia lateralis* was absent in ten out of the fifteen collections in 1951 and in January was absent from all five stations, but in 1952 it was absent from only three of the twenty collections and was taken in Sykeside and Outgate in every month. Therefore any collector who visited Ford Wood Beck during this period would have found all four commoner species if he had made only one collection at one place, but to make certain of the other two he would have had to come twice and collect in three stations each time.

Since there may be a large difference between the two halves of one collection (Table 1), it is not to be expected that a few collections will give a true picture of the proportions of the species. In 1951 either *Baëtis rhodani* or *Rhithrogena semicolorata* was always the commonest species, the former being in the lead four times out of the fifteen and numbers being equal once. Whichever of these two was not the most abundant occupied second place, except in three collections in which *Ecdyonurus torrentis* had it twice and *Baëtis pumilus* once. In 1952 the pattern is a little more constant. *B. pumilus* is second in abundance twice, but otherwise *B. rhodani* and *Rhithrogena semicolorata* are always the two most numerous species, though, in contrast to 1951, *Baëtis rhodani* is generally the most abundant, being first in seventeen out of the twenty collections. The conclusion is that a single collection can give a quite misleading impression of the relative abundance of the various species, but this is corrected by an unexpectedly small number of further collections.

COMPARISON WITH OTHER HABITATS

(*a*) *Stony streams and rivers*

Table 6 presents the results of ten-minute collections made by the writer in eleven becks in the Lake District, all of the same type as Ford Wood, though some are larger and some smaller, and a few rise at higher altitude. In nearly all fewer specimens were caught, and this is probably because all but the last two rise on uncultivated moorland, whereas Ford Wood Beck flows through agricultural land throughout its length and has only one tributary rising on untilled ground. The proportions of the species are not the same but the species list differs very little from that of Ford Wood Beck.

Table 7 presents the results of other workers. It is not possible to use all the

Table 6. *Results of ten-minute collections in Lake District becks*

	Station	Altitude of source (m)	Type	Drainage area (ha)	Number of collections	Date	*Ecdyonurus torrentis*	*Rhithrogena semicolorata*	*Heptagenia lateralis*	*Ecdyonurus venosus*	*Ephemerella ignita*	*Baëtis rhodani*	*B. pumilus*	*Paraleptophlebia submarginata*	*Ameletus inopinatus*	*Baëtis scambus*	*Siphlonurus lacustris*
Smooth		230	flowing out of tarn	120	3	20 October 49	7	–	–	–	–	–	–	8	–	–	–
						15 December 49	12	2	–	–	–	1	–	–	–	–	–
						30 June 50	3	2	3	–	5	16	23	–	–	–	–
Nor Moss	1	220	,,	150	3	18 April 50	–	45	13	–	a	2	11	a	–	–	–
	2				2	18 April 50	2	35	2	–	–	22	3	–	–	–	–
	3				3	18 April 50	9	7	–	–	a	12	4	a	–	–	–
Hog House	2	150	,,	125	2	16 May 50	28	4	–	–	a	a	13	2	–	–	–
	3				2	16 May 50	1	–	13	–	–	19	6	1	–	–	6
Pull	1	275	long beck like Ford Wood	150	1	16 May 50	3	46	–	–	–	61	12	–	–	–	–
	2				1	16 May 50	7	51	–	1	–	64	19	–	–	–	–
Dan	2	130	flowing out of tarn	110	2	9 May 50	a	116	–	–	a	57	5	–	–	–	–
	3				2	9 May 50	5	26	–	–	a	14	3	–	–	–	–
High Wray	1	225	steeper than Ford Wood	125	4	24 March 50	1	115	5	–	–	56	16	a	–	–	–
	2				4	24 March 50	1	28	13	–	–	8	8	a	–	–	–
	3				4	23 May 50	–	6	23	–	–	10	38	–	–	–	–
Holbeck	1	420	longer and bigger than Ford Wood	330	4	28 March 50	–	53	21	5	a	56	a	a	–	–	–
	2				5	8 May 50	1	11	31	a	–	12	a	–	–	–	–
	3				5	28 March 50	–	19	57	4	–	49	31	a	6	–	–
Stock Ghyll	1	530	,,	1 120	4	21 March 50	1	24	43	13	a	121	a	a	–	a	–
	2				4	16 May 50	–	31	11	13	a	110	a	–	a	a	–
	3				1	22 June 50	–	–	2	–	–	5	65	–	–	–	–
Whelpside	1	930	steeper than Ford Wood	110	1	28 May 51	–	58	1	3	–	70	1	–	7	–	–
	2				1	28 May 51	–	9	–	–	–	32	9	–	24	–	–
	3				6	28 May 51	–	1	–	–	a	3	–	–	9	–	–
						17 April 52	–	–	1?	–	a	9	–	–	28	–	–
						19 May 53	–	2	–	–	a	236	4	–	253	–	–
BH 1			shorter than Ford Wood	10	1	19 April 50	–	15	1	–	–	10	23	–	–	–	–
BH 2				25	1	19 April 50	–	61	44	–	–	4	18	–	–	–	–
Number of times present							15	24	17	7	12	27	24	10	7	2	1
Total number caught							81	767	284	39	5	1059	312	11	327	–	6

When several collections were made at one station and they were not dissimilar, only one is quoted, and any addition to the species list made on another occasion indicated by a. Station 1 is always the lowest station as in Ford Wood Beck.

published surveys because the earlier writers were not able to identify every one of their species; the first comparative account of species in the genus *Baëtis*, ecologically, as will be shown shortly, one of the most significant genera, was not published till 1950 (Macan 1950) and it dealt only with the British species. Only partial comparison can, therefore, be made with, for example, the findings of Eidel (1933).

Table 7. Ephemeroptera *in small stony streams*

× indicates the common species; + those less common; § taken only in a stretch with *Sparganium*.

	Present findings	Harker 1953	Illies 1952	Dittmar 1955
Rhithrogena semicolorata	×	×	×	375
Baëtis rhodani	×	×	×	106
B. pumilus	×	–	×	45
Ecdyonurus torrentis	×	×	–	–
Heptagenia lateralis	×	×	–	15
Ephemerella ignita	×	+	+	76
Paraleptophlebia submarginata	+	+	+	3
Ecdyonurus venosus	+	–	×	53
Centroptilum luteolum	§	–	+	–

Other studies, such as some of those made by Dr J. R. Erichsen Jones in Wales, have had to be left out because they were made in the summer months. Of the three streams in Table 7, Harker's was in southern Lancashire and those of Illies and Dittmar in western Germany. Illies found three species unknown in Britain, *Habroleptoides modesta* (Hagen), which was one of the commonest, *Habrophlebia lauta* McLachlan and the Ecdyonurid *Epeorus assimilis* Eaton. Dittmar (1955), who incidentally gives a valuable synopsis of the views of other continental workers on the habitats of the various species, found these three and six more non-British species as well as six British ones not listed in Table 7. It is clear from his notes that these last are from quieter parts of the stream, where there is a muddy bottom or rooted vegetation. Geijskes (1935), in a stream which differed from all just mentioned in being calcareous, did not find *Baëtis rhodani*, *Ecdyonurus torrentis*, *Heptagenia lateralis* or *Paraleptophlebia submarginata*. He recorded the remaining five of the species in Table 7 and in addition *Baëtis bioculatus* but again there is doubt about the identification of species in this genus.

Ecdyonurus torrentis has not been found outside Britain, and all the continental authors record *E. venosus* in small streams. In some of the streams in Tables 6 and 7 there are absences for which there is no explanation, but, with these exceptions, it may be said that small stony streams are typically inhabited by:

Baëtis rhodani
Rhithrogena semicolorata
Ecdyonurus torrentis or *venosus*
Baëtis pumilus
Heptagenia lateralis
Paraleptophlebia submarginata
Ephemerella ignita

In Table 8 collections from three inflows and one outflow (River Leven) of Windermere are presented and in Table 9 published records from one Welsh (Rheidol) and three Pennine rivers. All the beck species are present, but *Ecdyonurus torrentis* has been replaced almost completely by two other species. In the

Table 8. *Results of ten-minute collections in four Lake District rivers*

	Bottom	Drainage area (ha)	Number of collections		*Rhithrogena semicolorata*	*Baëtis rhodani*	*B. pumilus*	*Ecdyonurus torrentis*	*Heptagenia lateralis*	*Ephemerella ignita*	*Paraleptophlebia submarginata*	*Ecdyonurus venosus*	*Baëtis scambus*	*Ecdyonurus dispar*	*Heptagenia sulphurea*	*Centroptilum luteolum*	*Procloëon rufulum*	*Siphlonurus lacustris*
Brathay	stable	5600	10	July 1950	–		–	–	1	39	–	–	1	8	–	7	32	–
				Oct. 1950		23	3	–	1	–	1	2	–	–	5	–	–	–
				June 1951			24		–	–	–	3	–	–	19	4	–	2
				July 1951		–	3	–	–	182	–	–	–	7	6	2	47	1
				Dec. 1952		24	1	–		–		8	–	–	4	32	–	–
				Aug. 1953		5	7	–		86		15	65	–	–	2	–	–
Rothay	unstable	6200	7	July 1950	–		–		1	167	–	4	2	–	5	–	–	–
				Oct. 1950		86	–	–			–	7	1	–				–
				June 1951		1	–	–	–	9	–	16	21	–	–		–	–
				Dec. 1952	1	55	–					10	–			2	–	–
Troutbeck		2400	4	Mar. 1950	a	1	a	7	?	–	1	5	–	–	?	–	–	–
				June 1950		–	a	–	?	67	–	3	11		?	–	–	–
Leven	unstable	24 300	2	June 1950		18	a	–	?	248	–	–	11	–	?	a	–	–
		Total			1	213	38+	7	3+	798	2	73	112	15	39	49+	79	3

a = taken on another occasion.

Lake District rivers, though not in all the others, some of the common stream species, notably *Rhithrogena semicolorata*, *Heptagenia lateralis* and *Paraleptophlebia submarginata* were scarcer, whereas *Ephemerella ignita* was more abundant. The main difference is the presence in rivers of more species, the important newcomers being

Baëtis bioculatus
B. scambus
Heptagenia sulphurea
Centroptilum luteolum
Procloëon rufulum
Centroptilum pennulatum

The inclusion of the three species in the right-hand column is possibly more in the nature of a prophecy than a warrantable deduction from the facts in Tables 8 and 9. Having learnt how to recognize them (Macan 1949*b*), the writer recorded two of them during a short visit to the Tees, a river that had been worked very thoroughly, and has taken them often in other rivers. Pentelow based his list of Tees species on adults that he collected from the bank and quite likely missed at least *Procloëon rufulum* because, as Harris (1952) points out, it flies at dusk.

Table 9. *Collections in stony rivers by other authors*

×, abundant; +, present; p, present but abundance not determined since identification based only on adults; sp., species not determined.

	Lake District rivers (summary of Table 8)	Tees (Butcher, Longwell & Pentelow 1937)	Rheidol (Jones 1949)	Aire, Nidd, Wharfe (Percival & Whitehead 1929)	Wharfe (Percival & Whitehead 1930)
Baëtis rhodani	×	p	p	×	×
Ecdyonurus venosus	×	p	p	×	×
Baëtis scambus	×	–	p	–	–
B. bioculatus	–	p	–	×	×
Ephemerella ignita	×	×	sp.	×	×
Rhithrogena semicolorata	×	×	×	×	×
Baëtis pumilus	+	p	p	×	×
Heptagenia lateralis	+	p	×	×	–
H. sulphurea	+	p	–	×	×
Paraleptophlebia submarginata	+	sp.	sp.	–	–
Centroptilum luteolum	+	p	–	–	+
Ecdyonurus dispar	+	p	–	–	–
Procloëon rufulum	+	+*	–	–	+
Siphlonurus lacustris	+	sp.	×	–	–
Baëtis vernus	–	+	–	–	–
Leptophlebia sp.	–	–	+	–	–
Rhithrogena haarupi	–	p	–	–	–
Ephemerella notata	–	–	–	–	+
Paraleptophlebia cincta	–	–	–	–	+
Centroptilum pennulatum	–	+*	–	–	–
Habrophlebia fusca	–	+	–	–	–

* Nymphs recorded by me in August 1951.

(*b*) *Slow rivers*

When collecting from slow rivers with rooted vegetation, the writer has been seeking specimens for taxonomic study, and not making a survey, and there is only one major published survey (Berg 1948). The information is, therefore, somewhat incomplete, but, such as it is, it is set out in Table 10. The striking contrast with swift stony rivers is, as might be expected, the paucity of flat stone-clinging Ecdyonuridae, *Heptagenia sulphurea* being the only representative. On the other hand, in the genus *Baëtis* all the species already encountered are present and the difference lies in the fact that there are new species, *Baëtis vernus* and *B. tenax*, if these really are two separate species, and *B. niger*, a species with a wide range but confined, in the author's experience, to places with rooted plants.

If, now, by way of summary we postulate an imaginary river that is formed by the union of little mountain streams, and runs swiftly for a while but finishes up meandering through flat rich country in a bed with plenty of plants, we may expect the succession of Ephemeroptera to be as follows. Of seven species in the small stony streams, four may be expected to stretch right down to the point where flow becomes sluggish and vegetation thick. *Ephemerella ignita* becomes more abundant all the way, the others less numerous and the two species of *Baëtis* are joined and gradually exceeded in numbers by other members of their genus. The other three of the seven are all ecdyonurids and do not get so far. *Rhithrogena* persists as long as the current is swift, but *Ecdyonurus torrentis* is truly a species of small streams and is replaced by other species of the genus as streams become larger. *Heptagenia lateralis* is probably replaced by *H. sulphurea* as conditions become richer. Eventually species of *Cloëon*, typical pond-dwellers, predominate These relationships are expressed diagrammatically in Fig. 5.

Table 10. *Collections in slow weedy rivers*

The number of + symbols gives a rough indication of the degree of abundance; sp., species not identified.

	Avon*	Kennet	Cam	Yare	Wensum	Susaa†
Time spent	6 weeks 23 April-8 June 39	1 week 11 June-16 June 51 23 May 54	1 day 25 May 50	1 day 11 July 51	1 day 11 July 51	5 years
Baëtis tenax/vernus	++	+++	++	+++	+	+++(?)
B. bioculatus	+	++	–	+	++	–
B. scambus	–	+	–	–	–	+++
B. pumilus	++	–	–	–	–	–
B. niger	+++	+	–	–	–	–
B. rhodani	+	+	++	–	–	–
B. atrebatinus	+	+	–	–	–	–
Centroptilum luteolum	+++	++	–	–	++	++
C. pennulatum	–	+	–	–	–	–
Procloëon rufulum	+	–	–	–	++	–
Ephemerella ignita	++	++	–	++	–	+
Paraleptophlebia submarginata	+	+	–	–	sp.	–
Heptagenia sulphurea	+	+	–	–	–	+
H. fuscogrisea	–	+	–	–	–	+
Leptophlebia marginata	+	–	–	–	–	–
L. vespertina	–	–	–	–	–	+
Cloëon dipterum	–	–	–	–	–	++
C. simile	–	–	–	–	–	++

* Macan & Macan (1940).

† Berg (1948). *Cloëon inscriptum*, unrecorded in Britain, was also taken in the R. Susaa.

(c) *Slow streams*

Here too the information is scanty. *Siphlonurus lacustris* occurs in Holbeck in a reach near the top where there is very little fall, in a small sandy-bottomed tarn with a good flow through it at about 700 m (2100 ft) near Helvellyn in the Lake District, and in the ditch fed by underground water and therefore probably cold, mentioned on p. 326 above. On the other hand, before 1939, the top rather level stretch of Nor Moss Beck, now swifter owing to drainage, harboured *Leptophlebia marginata*, *L. vespertina* and *Paraleptophlebia submarginata*. Dittmar records all four together, and Eidel (1933) classes these three and *Siphlonurus aestivalis* as typical of the quiet places in his mountain stream. In the Lake District it seems as if *S. lacustris* is a cold-water form, but it is characterized by sporadic occurrence and any quick judgment would be rash. It was taken also in the River Brathay at a point where it runs slow and deep with little vegetation and in a similar river connecting Loch Loyal and another loch in Sutherland, while *S. armatus* was caught in the River Winster in Westmorland, and *S. linnaeanus* in the River Cree in Kirkcudbrightshire in much the same sort of place.

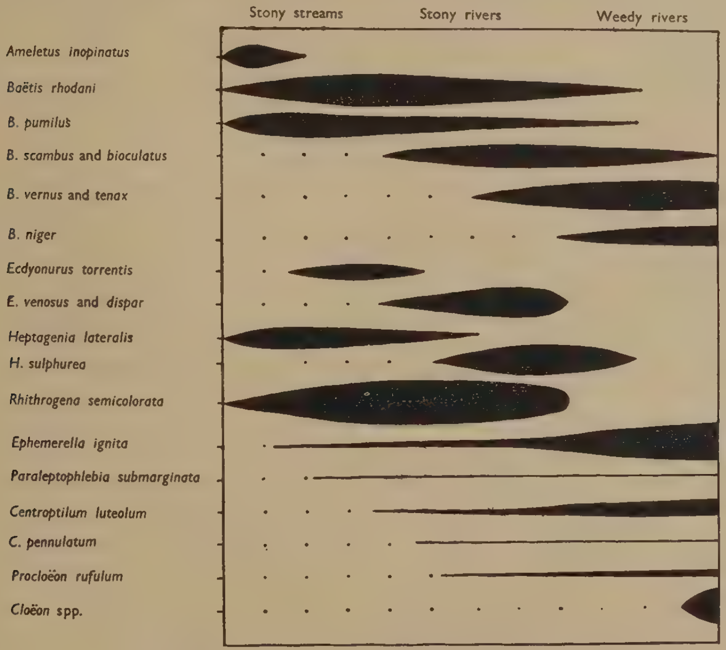

Fig. 5. Schematic representation of the population of Ephemeroptera in a river that starts as a mountain stream and ends flowing sluggishly through rich land.

Hog House is the only Lake District beck known to the writer that flows over a flat plain at the end of its course. It has a sandy bottom with stones, packets of dead leaves and tufts of vegetation here and there. Ephemeroptera are few in number generally, but at one time or another a large number of species has been found. They are *Baëtis rhodani*, *B. pumilus*, *B. niger*, *Centroptilum luteolum*, *C. pennulatum*, *Habrophlebia fusca*, *Paraleptophlebia submarginata* and *Ecdyonurus torrentis*. *Habrophlebia* was abundant on one occasion and this stream is not unlike Daggon's Brook where Macan & Macan (1940) found it in Hampshire. Mrs Mackereth has found it in a small stream flowing into the River Ribble which was more muddy than Hog House Beck but of the same type.

Albrecht (1953), in a moderately calcareous stream (35-80 mg CaO/litre) with a predominantly sandy bottom, found only *Ephemerella ignita*, *Paraleptophlebia submarginata*, *Heptagenia sulphurea*, *Baëtis rhodani* and *Baëtis* spp. Beyer (1932), surveying an area with many springs, water sufficiently hard for a calcareous crust to form on the bottom and mainly sandy substratum found *Heptagenia lateralis*, *H. sulphurea*, *Baëtis bioculatus*, *Ephemerella ignita*, *Cloëon dipterum* and two species that do not occur in Britain, *Heptagenia flava* and *Siphlonurus aestivalis*. More collecting in places of this kind must be done before such divergent results can be connected.

(*d*) *Stony lakes*

Ecdyonurus dispar and *Heptagenia lateralis* occur on the stony shores of Windermere; as the writer has collected over 200 specimens of *Ecdyonurus* in this lake without seeing *E. venosus*, he believes that Moon's (1934) record of it is due to misidentification. *Heptagenia sulphurea* and *H. fuscogrisea* are found on the stones of limestone lakes in Ireland (Harris 1952). *Centroptilum luteolum* often occurs on exposed lake shores, *Ephemerella ignita* very occasionally (Macan & Lund 1954), and in several lochs in the north of Scotland the writer has taken fair numbers of *Ameletus inopinatus*.

This is a small species list compared with that of a similar substratum in running water, the genera *Baëtis*, *Rhithrogena* and *Paraleptophlebia* being unrecorded. In quieter conditions where there are weeds the number of species is also small: *Leptophlebia marginata* and *vespertina*, *Cloëon dipterum* and *simile*, and *Siphlonurus lacustris* and *linneanus*.

REMARKS ON INDIVIDUAL SPECIES

Ameletus inopinatus is a stream species found only at high altitudes (Table 6, Eidel 1933). The fluctuation in number from year to year is greater than any in Ford Wood Beck. The highest temperature on a maximum and minimum thermometer at 600 m (2000 ft) in Whelpside Ghyll was 15·6° C in August 1950, compared with a maximum of 19° C in Outgate Beck.

Ecdyonurus torrentis was found only in the Lake District becks (Table 6), in one Lake District river (Table 8), and in Harker's beck (Table 7). The first three becks in Table 6 are the three with most *E. torrentis* and all originate in, or flow through, tarns. In both Nor Moss and Hog House Becks the biggest catches of *E. torrentis* were at stations just below tarns. Where this species was most numerous other members of the family Ecdyonuridae were at their scarcest. The predominance of

E. torrentis in these places and in the lowest reach of Ford Wood Beck might be due to the better food supply that is likely to be found at the end of a beck or just after it has come from a tarn laden with the plankton that grows in still water. On the other hand, it might be correlated with the higher maximum temperature to be expected under such conditions. That *E. torrentis* was most abundant in Ford Wood, the beck that was most favourable for all species, supports the food hypothesis.

Ecdyonurus venosus and *E. dispar* replace *E. torrentis* completely in all but one of the rivers (Tables 8 and 9), and the former largely replaces it in two of the largest becks (Table 6). Since during collections to obtain material for taxonomic studies *E. dispar* was found in the Rivers Eden (CU), Lune (ML), Tees (NY) and Mole (SR) and *E. venosus* only in the Rivers Eamont (CU) and Eden (WL), it is hard to resist the conclusion that the scarcity of *E. dispar* in Table 9 is due to taxonomic trouble with this difficult group; the nymphs of the British species were first distinguished by Kimmins (1942) and described again by Macan (1949*a*).

Rhithrogena semicolorata. In the two Lake District becks in which it is scarce, Smooth and Hog House (Table 6), there are fair numbers of *Ecdyonurus*. That it is abundant at stations 2 and 3 and *Ecdyonurus* at station 1 in Ford Wood Beck also suggests competition between the two. In the other becks *Rhithrogena* tends to be the more abundant the farther down the stream, which is what Illies (1952) and Dittmar (1955) find, though in their becks decreasing abundance of this species upstream goes hand in hand with increasing abundance of *Ecdyonurus venosus*. *Rhithrogena* was found throughout the upper half of the River Tees, often in abundance, but was scarce below the confluence of the Skerne, a polluted tributary below which there were growths of sewage fungus and *Cladophora* which trapped silt in summer. *Ecdyonurus* spp., which includes *Heptagenia lateralis*, were the main ecdyonurids below the confluence. Percival & Whitehead (1930) write: '*Rhithrogena* is found dominant in those regions where there is a very rapid flow, with rounded smooth stones which have no visible vegetation and present evidence of movement during flooding. *Ecdyonurus venosus* appears when the bed becomes more stable, and with increasing stability *Rhithrogena* disappears while *Ecdyonurus* increases.' Harker (1953) found crushed bodies of *Ecdyonurus* and *Heptagenia* but not *Rhithrogena* in drifts after floods. Strenger (1953), after close comparison of its morphology with that of *Ecdyonurus*, concludes that *Rhithrogena* is better fitted to withstand strong current. In spite of all this evidence, I doubt whether the distribution of *Rhithrogena* is determined entirely by current speed and stability of bottom. In Ford Wood and other Lake District becks there are no marked differences in the substratum occupied by the two species, and it seems more likely that certain conditions of food or possibly temperature favour *Ecdyonurus* at the expense of *Rhithrogena*. If *Rhithrogena* is typically a species of the unstable bottom, it should occur in the River Rothay, where it has not been found (Table 8). The Tees observations are difficult to evaluate because the Tees had a decreased average fall below the confluence of the Skerne.

Heptagenia lateralis in the Lake District (Table 6), was not found in Dan Beck or Pull Beck, the two most like Ford Wood, but occurred in all the others, in some in much greater abundance than in Ford Wood. It was commonest in two, Holbeck and Stock Ghyll, that rose fairly high up, but only one specimen was taken in Whelpside Ghyll, the third stream in this category. This last, however, being a good deal steeper than the other two, was not strictly comparable with them. Percival & Whitehead (1929) write that it is 'often found in the same stream as *Ecdyonurus venosus*, but normally occurs along the edges in small bays and other places where the current is much reduced . . . This nymph is more usually found, in Yorkshire, in the upper part of streams towards the moors. It is quite abundant at altitudes varying from 200 ft to 2000 ft.' On the whole, the Lake District collections support this idea that it is a species of the upper parts of moorland becks. Pleskot (1953) records it as one of the commonest and most widely distributed species in Austria, it was scarce in the streams studied by Illies and Dittmar, and Eidel found it in the lower reaches of a Swiss stream. Jones (1949) found it abundantly in the lower parts of the Welsh River Rheidol. In conversation, Dr Jones has pointed out that the lower reach, where the current slackens a little, of a river of this kind, which flows swiftly down a barren mountainside, may resemble the slow upper reach in its barrenness and low temperature. Harker (1953) found that floods affected this species more than other ecdyonurids, but if this is a major factor in its distribution, it is difficult to explain why it was most abundant in Holbeck, which is one of the steepest of the Lake District streams studied.

Baëtis rhodani is absent from only one station in the Lake District becks (Table 6), a station in a beck with a sparse ephemeropteran fauna throughout. In the other becks and in the rivers it is generally among the abundant species and often the commonest. The difference in size of the catches in three successive years in Whelpside Ghyll (Table 6), much greater than any seen in Ford Wood Beck, is a reminder of the danger of basing conclusions on a small number of collections.

Baëtis pumilus, though not often absent, was generally distinctly less abundant than *B. rhodani*. In three of the Lake District becks, High Wray, Holbeck and Stock Ghyll (Table 6), where fairly large captures were made, they were at the highest of three stations, but the species was not more abundant in the upper reaches of Ford Wood Beck, or Whelpside Ghyll, which, however, is steeper than the rest. Geijskes (1935, p. 329) calls it a crenophil, that is a species dwelling by preference (vorzugsweise) but not exclusively in springs. In Dittmar's (1955) stream it is one of the two species actually to occur in the springs, it reaches its greatest abundance just below them in the 'Quellbach' zone where all others are scarce, and is one of the more numerous species as far down as the stream was studied. Illies's (1952) findings are similar except that *B. pumilus* was scarcer and did not reach as high as the 'Quellregion'. Illies calls it 'mässig stenotherm' but according to Pleskot (1954) it is 'eurytherm'. Pleskot describes it as 'fissikol', that is inhabiting the interstices of the substratum. If nymphs crawl between the smaller stones when small and come out on to the bigger ones when large, just such an increase in catch as was obtained (Fig. 3) would be expected.

Ephemerella ignita was found in all the becks which were searched during appropriate months (Table 6). In Stock Ghyll and Holbeck, as in Ford Wood Beck, it was not taken from the upper reaches, but a few specimens, four altogether, were found at station 3 at 600 m (2000 ft) in Whelpside Ghyll in 1951 and 1952. It was more numerous at the top of Nor Moss Beck than lower down, but Nor Moss is one of the becks that flows from a tarn, and it has already been argued that conditions downstream of a tarn have something in common with conditions at the end of a stream. This species can live under stones, as in Ford Wood Beck, but is much more numerous where there are higher plants or moss, especially in rivers.

Paraleptophlebia submarginata was very scarce at all stations except one in the Lake District becks (Table 6) and was not found in five. The exception was station 3 of Nor Moss Beck, where the gradient is relatively slight, suggesting that optimal conditions for this species are in conditions more sluggish than those in stony streams. Eidel, Illies and Dittmar corroborate this.

Baëtis scambus in the Lake District rivers and the River Rheidol, and *B. bioculatus* in the more calcareous Pennine waters (Table 9) are two river species that seem to be vicarious. The irregular appearance of *B. scambus* in successive years in the River Brathay (Table 8) is worth noting. The life history is unknown, but nymphs have never been taken in the winter, so it may be unlike that of *B. rhodani* and *B. pumilus*.

Heptagenia sulphurea occurs sparingly in the Lake District becks and abundantly in the Pennine rivers (Table 9). Pleskot (1954) records it as common in the big rivers of the plains of Germany.

Siphlonurus lacustris has been discussed in the section on slow streams.

Centroptilum luteolum, *C. pennulatum* and *Procloëon rufulum* are all associated with quiet sandy and gravelly bays and backwaters.

Rhithrogena haarupi, *Ephemerella notata* and *Paraleptophlebia cincta* are species that have been captured only a few times.

DISCUSSION

A detailed study of a small stony stream revealed seven species, four of them plentiful, the three others less so. In other streams were found the same species and an eighth, *Ameletus inopinatus*, confined to high altitudes. On the same sort of substratum in a larger piece of water, there are different species of *Ecdyonurus* and, lower down, of *Heptagenia*, and a greater number of species. Farther on in a river, where current becomes slow enough for the settling of silt and the consequent growth of vegetation, there is a marked change in the fauna, the stone-clinging ecdyonurids disappearing and some weed-dwelling species appearing. On stony shores in lakes many running-water species have never been found.

Ide (1935) chose a series of stations down a Canadian stream that were as similar as possible except in temperature, each being warmer than the one above. A few species at the top did not extend down to the lowest stations but, in spite of this, the species list grew longer with progress downstream. Ide attributes it all to temperature, the river becoming lethally warm for certain cold-water species confined to the top, and being insufficiently warm in the upper reaches for certain species that occurred lower down to complete development. British rivers offer an exact parallel; *Ameletus inopinatus* is confined to the upper reaches, and lower down there are more species. Ide's explanation may account for the distribution of some species, but it is difficult to believe that it is quite as comprehensive as he would have it. For one thing, however similar the substratum may remain, a stream grows larger as it progresses, and larger size may mean that everything is on a larger scale. For example, a sandy bay beside a stream may provide the right conditions for one nymph of *Centroptilum luteolum* whereas a similar bay lower down on a larger scale may provide the right conditions for a colony large enough to perpetuate itself.

Substratum may be one of the most important factors. Hynes (1941) has described differences in the Plecoptera of stable and unstable stream and river beds, and similar differences in the Ephemeroptera were mentioned above when *Rhithrogena semicolorata* was being discussed. For Ephemeroptera, at least, the classification of Percival & Whitehead (1929) based on types of substratum seems to lead to a better understanding of distribution than the classification based on temperature which Illies (1952) and Dittmar (1955) use.

Rate of flow must be a factor of importance, and Harker's findings that a flood affects *Heptagenia* most, *Ecdyonurus* less and *Rhithrogena* least have already been mentioned. *Paraleptophlebia submarginata* was one of the less numerous species in Ford Wood Beck and evidence has been produced that optimum conditions for it are in a stream with slower flow. Likewise, *Centroptilum luteolum* occurred only in the slowest part of Ford Wood Beck. But it would be interesting to know more about exactly how swift current limits range, for all the nymphs live on the bottom under or between stones in places where there cannot be much current. *Ephemerella ignita*, which reaches its greatest abundance in weeds in slow water, manages to maintain a small colony in Whelpside Ghyll, which is nearly as steep as a stream can be without being a cascade.

Of oxygen it is difficult to speak because the critical value is likely to be, not the average, but a minimum that may occur for only a short period once or twice a year. The absence of *Baëtis* and other genera from stony bottoms in still water may be due to inferior oxygen conditions, but until much more is known about the fluctuation of oxygen concentration this can be no more than supposition.

The difference between the fauna of English soft-water and Irish calcareous lakes suggests that calcium is an ecological factor of significance, though how it influences a species is unknown.

ACKNOWLEDGMENTS

The assistance of Mrs Jean C. Mackereth is gratefully acknowledged. I have also to thank Miss R. M. Badcock for making flow measurements with a current meter.

SUMMARY

1. Collections with a pond-net were made once a month from five stations in a small stony stream. Collections were often in two parts and the difference between the catches in each part is discussed.

2. The common species were *Baëtis rhodani*, *Rhithrogena semicolorata*, *Ecdyonurus torrentis*, *Baëtis pumilus*, *Heptagenia lateralis*, *Ephemerella ignita* and *Paraleptophlebia submarginata*.

3. *Ephemerella* nymphs are found only in a few summer months, at which time some of the others are scarce or absent. A true picture of the fauna of a stream cannot be obtained unless collections are made twice: in July or August and again some time during the first five months of the year.

4. Fluctuations in numbers from year to year were not great.

5. *Ephemerella* occurred only in the lower reaches, but all the other species inhabited the whole of the region investigated. The four commoner species were more abundant in the lower, the two less common (*Paraleptophlebia* and *Heptagenia*) in the upper reaches. *Ecdyonurus* was most plentiful near the mouth, *Rhithrogena* a little higher up.

6. The populations of the three lowermost stations in the first five months of the year were sufficiently similar to be used as a basis to determine the least amount of collecting that would have revealed a picture like the one found. A single collection could have given a very distorted picture of the composition of the population but it would have been corrected by quite a small number of further collections. Visits in two different months to all three stations would have been necessary to make certain of collecting all seven species.

7. Comparison with other streams in the Lake District and with published work confirms that the species mentioned are typical of small stony streams except that *Ecdyonurus venosus* replaces *E. torrentis* outside Britain.

8. Similar comparison is made with stony rivers. *Ecdyonurus torrentis* is replaced by other species in the same genus, but otherwise the difference is in the appearance of new species, notably *Baëtis scambus*, *B. bioculatus*, *Heptagenia sulphurea*, *Centroptilum luteolum*, *Procloëon rufulum* and *Centroptilum pennulatum*.

9. In those reaches of a river sluggish enough for the deposition of silt and the establishment of rooted plants, the ecdyonurids are not found, though *Heptagenia sulphurea* persists longer than the others, but otherwise the difference is one of addition. *Baëtis vernus*, *B. tenax* and *B. niger* occur with the species found in the higher stony reaches.

10. There are rather big differences between the lists of species that have been recorded from slow streams.

11. The list of species on stony lake shores (*Ecdyonurus dispar*, *Heptagenia*

lateralis, H. sulphurea, H. fuscogrisea, Centroptilum luteolum, occasionally *Ephemerella ignita,* and, in the far north of Scotland, *Ameletus inopinatus*) is much shorter than that on a similar substratum in running water, the genera *Baëtis, Rhithrogena* and *Paraleptophlebia* being notable absentees.

12. The habitats of the various species are discussed.

13. Some speculations about the factors causing the distributions found are made.

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NOTES ON THE PLECOPTERA FROM A STONY STREAM

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(With 2 Figures in the Text)

Quantitative collections were made for three years in Ford Wood Beck, a small stony stream, and its tributaries, Sykeside and Outgate. The main objective of these collections was the study of the Ephemeroptera (Macan 1957). Plecoptera were not of the same interest because Hynes (1941) made many observations on them in this district, but a study confined to one stream for so long does bring to light certain facts that the more random collecting of Hynes and also of Brinck (1949) did not, notably differences in relative and absolute numbers in different parts of the stream and in successive years. Also, since quantitative collections of the whole fauna were made, it was possible to make a comparison between what was eaten and what there was to eat which was more accurate than that of previous workers. It is these aspects of the findings that are discussed in this paper.

The stream, stations and collecting techniques have been described by Macan (1957). Five stations, three in the main stream, numbered serially from the mouth upwards, and one in each of the tributaries (SS and OG), were visited monthly, and station 4 near the source of the main stream was included in 1951. Collections were made for a period of 10 min, or sometimes for two periods of 5 min, by washing the animals off the stones into the net of a pond net with 20 meshes/in. In October 1951 collections were made by using a net of much finer mesh. Collections were made with both nets for the following 14 months.

Sixteen species of Plecoptera have been recorded from the stream, and their names, which are those used by Kimmins (1950), are set out in Table 1. Hynes (1941, Fig. 19, p. 529) records all these species from similar streams in the area.

THE TOTAL CATCH

(*a*) *Distribution in time and place*

The data are presented in Table 1 and Fig. 1. Table 1 shows the totals caught per season or per calendar year, according to life history; collections were not made in every month in 1950 and the months omitted then have been omitted from 1951 and 1952 to make the totals strictly comparable. *Amphinemura sulcicollis*, *Nemoura cambrica* and *Leuctra fusca* all show marked increases in abundance, but the numbers of the other species altered little in successive seasons.

The numbers per station of *Chloroperla torrentium*, the only plentiful species for which there is not a histogram, were:

Station:	1	2	3	SS	OG
1950-51	24	11	23	2	17
1951-52	14	18	39	8	17

This species was distributed in the stream in a similar fashion in both seasons. A study of Fig. 1 shows that the same is true of all the other species except *Isoperla grammatica* which was most abundant in Sykeside in 1950-51 and, in the following season, less abundant there and more abundant at stations 1, 2 and 3.

In Table 2 the season's catch at each station is expressed as a percentage of the season's catch at all stations. *Perlodes mortoni* occurred mainly in Sykeside Beck, the only part of the stream liable to dry up, well over 50% of the total being taken there in both seasons. Percival & Whitehead (1928) state that the eggs of this species are not affected by 18 hours' drought in the laboratory. Hynes (1941) suggests that the small nymphs can survive a dry period in the damp gravel of the stream-bed. *Perla carlukiana*, on the other hand, with an aquatic life extending over three years, never occurred in Sykeside. It was also extremely scarce in Outgate Beck. *Isoperla grammatica* and *Chloroperla torrentium* were present at all stations, but wherever the percentage of one was high that of the other tended to be low. Numbers of *C. tripunctata* were so low that not much importance can be attached to them.

Table 1. *Total numbers of Plecoptera caught in Ford Wood Beck*

SPECIES GROWING IN WINTER

The figures show the total numbers caught at 5 stations, from August of one year to July of the next.

	1950-51	1951-52
Perlodes mortoni Klap.	40	42
Isoperla grammatica (Poda)	323	369
Chloroperla torrentium (Pict.)	77	69
C. tripunctata (Scop.)	6	6
Leuctra hippopus Kemp.	217	343
L. inermis Kemp.	70	175
L. nigra (Oliv.)	15	15
Protonemura meyeri (Pict.)	52	48
P. praecox (Mort.)	12	6
Amphinemura sulcicollis Steph.	25	232
Nemoura cambrica Steph.	288	1044
Brachyptera risi (Mort.)	24	20

SPECIES GROWING IN SUMMER

The figures show the totals each year at 5 stations for the months March and May to November inclusive.

	1950	1951	1952
Leuctra fusca Linn.	34	108	128
L. moselyi Mort.	1	5	1
Nemoura erratica Claas.	4	0	0
Perla carlukiana Klap.*	115	124	128

* *Perla carlukiana* takes three years to complete its development.

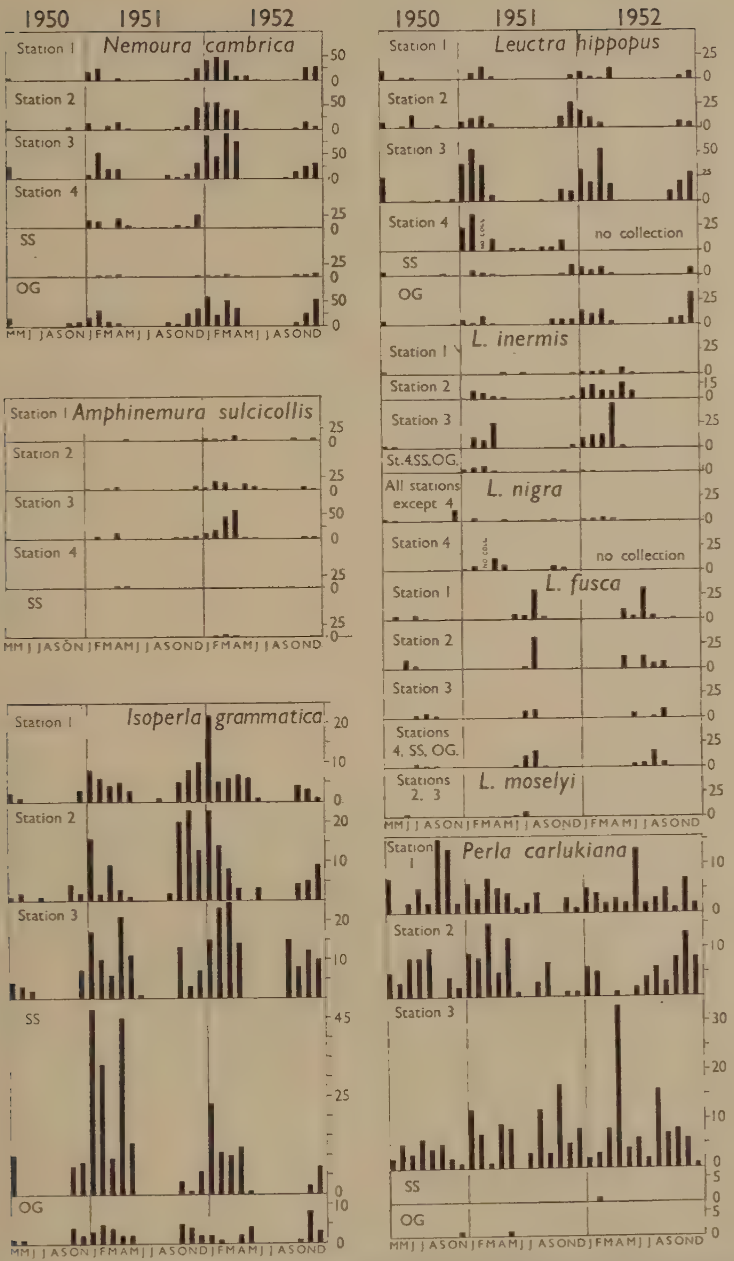

Fig. 1. Numbers of nine species of Plecoptera taken at the five stations in successive months.

There were eleven herbivorous species in the stream and Table 2 shows the distribution of the eight winter growers. All these species occurred at the stations in the main stream, and all but two were most abundant at station 3, where the water was more torrential than at any of the other stations. Four species were absent from Sykeside in the first season and five in the second, and all except *Brachyptera risi* were very scarce there. Only three species in the first and four in the second season were taken in Outgate Beck. It may be significant that the two species that occurred in both seasons, *Leuctra hippopus* and *Nemoura cambrica*, emerge in early spring whereas the rest emerge later, at a time when the level of both tributaries is generally low and when Sykeside may be dry. Sykeside might be expected to have a poorer fauna than Outgate, which may be reduced to a trickle but has not been known to dry up. Possibly the reverse is found because the population at station SS consists mainly of immigrants from station 3 a little downstream, where nymphs were numerous. By contrast immigration upstream into Outgate Beck may be hindered by a sheet of almost vertical flat rock face.

Table 2. *The distribution of the Plecoptera in Food Wood Beck in two successive seasons*

For the commoner species the figures show the totals caught at each station expressed as percentages of the total at all five stations; for the four rarer species the actual numbers are given.

	Season 1950-51						Season 1951-52					
	Station					Total	Station					Total
	1	2	3	SS	OG	Specimens	1	2	3	SS	OG	Specimens
CARNIVORES												
Perlodes mortoni	3	12	17	63	3	40	19	3	0	69	9	42
Perla carlukiana	35	38	26	0	1	180	22	17	60	1	0	186
Isoperla grammatica	8	11	23	52	6	323	17	21	34	22	7	369
Chloroperla torrentium	31	14	30	3	25	77	25	30	10	13	22	69
HERBIVORES												
Leuctra hippopus	10	16	64	3	7	217	9	22	38	11	22	343
L. inermis	6	30	61	2	0	70	10	41	46	2	1	175
Protonemura meyeri	27	12	57	0	4	52	53	7	30	0	0	48
Amphinemura sulcicollis	4	28	64	4	0	25	9	26	65	0	0	232
Nemoura cambrica	17	16	35	2	30	288	17	25	34	1	24	1044
RARER SPECIES (actual numbers)												
Chloroperla tripunctata	1	0	5	0	0	6	0	3	3	0	0	6
Leuctra nigra	1	0	14	0	0	15	3	2	5	0	5	15
Protonemura praecox	6	6	0	0	0	12	1	2	3	0	0	6
Brachyptera risi	1	2	3	18	0	24	8	1	2	9	0	20

The remaining three herbivores have been omitted from Table 2 because they are summer growers. *Leuctra fusca* was fairly common in the main stream, and a few specimens were taken in Sykeside in 1951. Some specimens of *L. moselyi* were recorded from station 3 in 1950 and 1951 and of *Nemoura erratica* at station 1 in 1950.

Station 4 was not included until the work had been in progress for a year, and collections there in 1952 were made with the fine net only. The collections made in the twelve months of 1952 are shown in Table 3 and may be compared with the totals in the five other stations. Station 4 was in the main stream in a fairly steep part, but because it was above the confluence of the two main tributaries it carried less water. Moreover most of its water reached it after percolating through soil and therefore heavy rain produced an effect much less violent than in other parts of the stream. The result was that the stones were embedded in silt rather than coarse sand or gravel as were those elsewhere. Six species are more plentiful than might be expected in that their numbers are more than one-sixth of the total at all six stations (*Isoperla grammatica*, *Chloroperla torrentium*, *Leuctra hippopus*, *L. inermis*, *L. nigra*, and *Nemoura cambrica*), and the number of *Leuctra nigra* is some six times that at all the other stations together. Hynes (1941) records that it occurs in silty places.

Table 3. *Catches of Plecoptera with nets of different mesh in 1952*

	Stations 1, 2, 3, SS, OG		Station 4
	Coarse net	Fine net	Fine net
Perlodes mortoni	34	22	0
Perla carlukiana	204	120	14
Isoperla grammatica	335	360	178
Chloroperla torrentium	94	265	160
C. tripunctata	8	14	0
Brachyptera risi	20	4	0
Leuctra hippopus	382	552	448
L. inermis	169	296	156
L. nigra	12	24	132
L. moselyi	1	0	0
L. fusca	128	212	24
Protonemura meyeri	97	110	6
P. praecox	5	14	0
Amphinemura sulcicollis	234	240	66
Nemoura cambrica	1078	1840	1074
N. erratica	0	0	0

The general picture is thus of the main stream fairly uniformly populated, though most species occur in greatest numbers in the swiftest part. Near the top, where conditions are silty owing to a decreased volume of water, there is a change in the proportion of the species, marked in the case of *Leuctra nigra*. In a tributary that dries up, the fauna is similar except that the large carnivore is *Perlodes mortoni*, which takes one year to grow up, not *Perla carlukiana*, which takes three. In the other tributary, which closely resembles the main stream except that it carries less water and is possibly affected by the proximity of the peatmoss in which it rises, the fauna is similar to that lower down but much poorer in total specimens and total species. Possibly a long waterfall, preventing immigration, may contribute to this poverty.

It will be noted in Table 2 that three species of *Leuctra* have similar distributions with great abundance at station 3. This table, however, omits station 4, at which *L. nigra* is much more abundant than the other two; plainly its habitat is different. *L. hippopus* and *L. inermis*, however, seem to have similar habitats to judge from present results and those of Hynes (1941), but the former emerges before the latter

(Fig. 1 and Hynes 1940, Fig. 14) and therefore the two are separated in time, though not in space. *L. fusca* emerges later still, but whether the temporal isolation of breeding adults is as complete as Illies (1952) found is not a question to be discussed now, because catches with an emergence trap are still in progress.

(*b*) *Catches with nets of different mesh*

The coarse-mesh net caught more of the big species, *Perla carlukiana* and *Perlodes mortoni*, than the fine-mesh net (Table 3), probably because the more rapid flow of water through it made escape against the current more difficult. The fine net caught more of the small species, no doubt because it retained tiny specimens that went through the coarse one, but there were no really big differences such as were found among the Ephemeroptera (Macan 1957).

(*c*) *Collections in other streams*

Occasional ten-minute collections in ten streams like Ford Wood Beck revealed a similar though sparser fauna. At 600 m (2000 ft) in Whelpside Ghyll *Diura bicaudata* was abundant in winter and spring, *Isoperla grammatica* in summer, and this record is noteworthy because Hynes (1941) did not take the latter above 1000 ft. In another high stream, Stock Ghyll, *Perla carlukiana*, *P. cephalotes* and *Isoperla grammatica* but no *Diura bicaudata* were taken at three stations above 1000 ft.

FOOD

Fig. 2 shows the food of three carnivorous species, the numbers of each organism eaten being expressed as a percentage of the total organisms eaten. *Perla carlukiana* feeds predominantly on *Baëtis*; observations covering thirteen months have been separated into nine groups each comprising one or two months and *Baëtis* made up over 50 % of the animals eaten in every one except December of one year and November and December of the next. Its place as the main food organism was taken by *Simulium* and by *Rhithrogena* and *Simulium* in the two years respectively. As might be expected, *P. carlukiana* does not eat those caddis larvae which live in cases, nor *Ancylus*, nor the larvae or adults of helmid and helodid beetles, which live in the gravel. No flatworms were ever found inside a stonefly nymph but whether because they were not eaten or because their soft bodies were rendered unrecognizable very soon by the digestive juices cannot be determined.

The fauna was collected with a fine net and with a coarse net and the problem is now to decide which set of figures should be used for the comparison with what was found in the stoneflies. At station 3 in June nearly 5000 nymphs of *Baëtis rhodani* under 3 mm long were caught, and if the proportion of the various species in such a catch be calculated, all others contribute no more than a fraction of 1% of the total. The percentage of all those others would be higher in the *Perla* guts than in the catch, and the deduction would be that *Perla* selected them. The deduction would be wrong because the *Perla* does not eat the tiniest nymphs and therefore the two sets of percentages would not be calculated from comparable totals. On the other hand some of the smaller nymphs of *Baëtis* that *Perla* does eat pass through the coarse net. In the absence, therefore, of exact data on the size-groups eaten by *Perla*, which would be very difficult to obtain, it is not possible to draw up two columns of exactly comparable percentages, one for the contents of *Perla*, the other for the contents of the net. On the whole it seems preferable to use the figures obtained with the coarse net. The percentage of *Baëtis* eaten is then always considerably higher than the percentage caught by net. Some reduction of the difference must be made to allow for the specimens not caught by the net, but it seems likely that there is selection of *Baëtis*, which is unexpected since *Baëtis* is the only member of the fauna capable of sudden and rapid flight. The figures for *Rhithrogena* are more variable. In March and April it contributed 23% to the contents of the guts and 11% to the total fauna, in contrast to the preceding December when the figures were 5 and 25% respectively. Probably the number eaten depends on how many other animals there are to eat. *Simulium* larvae are undoubtedly selected, for they never formed more than 3% of the catch, but during the appropriate time of year they were always among the most numerous of the animals eaten. Their sedentary habit would presumably make them an easy prey for the big carnivores, and it is tempting to speculate whether their low numbers in the stream might be due to the scarcity of large boulders and rock faces washed by a flow so strong that the stonefly nymphs could not walk across them. It is not surprising that chironomid larvae also are more abundant in the food than in the fauna. On the other hand *Gammarus*, though always numerous in

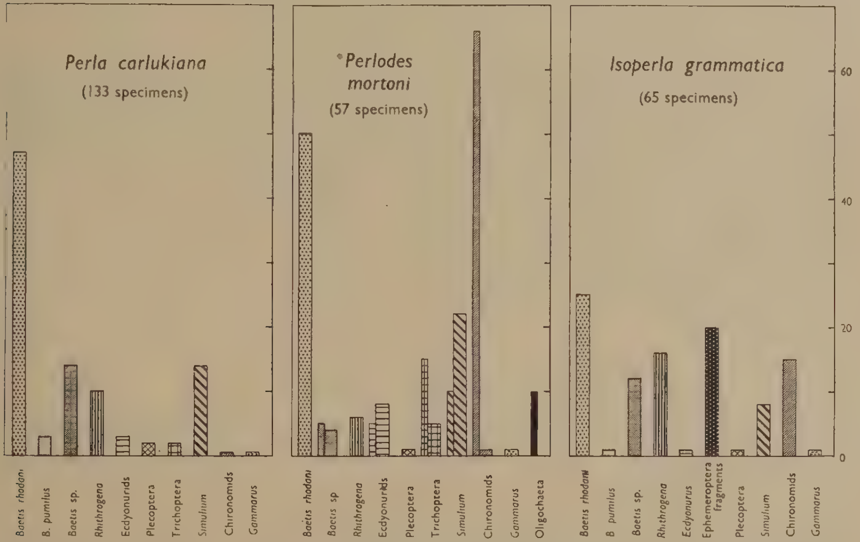

Fig. 2. The food of the three large carnivores. Each organism is shown as a percentage of all the organisms eaten. Ten specimens of *Perlodes mortoni* were less than 6 mm long; their food has been calculated separately and is shown to the left of that of the larger specimens.

the stream, is rare in the gut contents; evidently for some reason *Perla* has difficulty in finding or tackling it. Various Plecoptera and caseless Trichoptera are eaten in proportions that are probably related to their numbers,

From August to December inclusive the number of animals per nymph was between 2·7 and 4·7, a result which corresponds closely with that obtained by Jones (1950) for *Perlodes mortoni*. In the early months of the year the number ranged from 0·9 to 1·1. The percentage of nymphs with nothing or unidentifiable remains in them varied in a similar way. It is not possible to separate the various factors involved. In early summer a number of the empty nymphs will be those about to emerge, in January and February temperature may depress the rate of feeding, and in summer the results may be affected by quicker digestion and later collection relative to daybreak. Probably this last is not important, because in August, when emergence is over, the number of animals per nymph was 3, which is relatively high, and the number of empty ones was small.

Fewer specimens of *Perlodes mortoni* and *Isoperla grammatica* were opened, but their feeding habits appeared to be very similar to those of *Perla*. Small *Perlodes mortoni* had been feeding mainly on chironomids and had also found some oligochaetes, but it is not known whether this is general, for at the time when the ten were obtained the stream had only just started to flow again and lacked most of its characteristic inhabitants. The picture of *Isoperla grammatica's* food looks a little different at first sight but this is probably largely because many of the ephemeropteran remains could not be ascribed with certainty to a genus. It does, however, eat more chironomids and fewer *Simulium* than the other two species.

ACKNOWLEDGMENT

I wish to thank Dr T. T. Macan for help in the preparation of this paper.

SUMMARY

1. Five, and for part of the time six, stations in a small stony stream were visited monthly during a period of three years. Collections were made with a hand net used for ten minutes.

2. Sixteen species were found. Three became more abundant during the course of the work, catches of the rest varied little in size. Only one species showed a change in the pattern of abundance at the various stations.

3. The main part of the stream was rather uniformly populated, though most species were most numerous in the swiftest part. Near the top, several species, notably *Leuctra nigra*, were more abundant than elsewhere. A tributary which dried up in warm summers had a population similar to that of the main beck, except that *Perlodes mortoni* replaced *Perla carlukiana*. The other tributary was poor in numbers and species.

4. *Leuctra hippopus* and *L. inermis* appear to have the same habitat but emerge

at different times of year. *L. nigra* occurs with them but has not an identical habitat.

5. *Perla carlukiana* eats more *Baëtis*, *Simulium* and chironomids and fewer *Gammarus* than it would if its food were a random sample of the fauna. *Ancylus*, caddis larvae in cases, and animals that inhabit the gravel were not found inside it. The same is largely true of *Perlodes mortoni* and *Isoperla grammatica*.

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A PRELIMINARY SURVEY OF THE SMALL NATANT FAUNA IN THE VICINITY OF THE SEA FLOOR OFF BLYTH, NORTHUMBERLAND

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Compared to the very large volume of work done on the fauna of the pelagic and benthonic habitats in the sea, the small natant fauna immediately above the sea floor has received rather scant attention as an ecological entity. Nevertheless enough material has been accumulated by a number of workers all over the world at various times to indicate that this fauna is often both diverse in species and abundant in numbers, and undoubtedly plays an important role in the economy of the sea. Collections taken by Holt off Ireland, by Russell in the English Channel, and by Wilson off New England, all using fine nets mounted on or inside trawl nets (*e.g.* Russell 1928), should be especially mentioned in this connection (Holt & Tattersall 1905, Calman 1906, Tattersall 1906, Wilson 1932, p. 4, Tattersall 1938).

Important studies were also made by many authors on this fauna as a constituent of fish food, for instance Blegvad (1917), Hertling (1938), Shorygin (1952), to mention only a few. Greze (1951) used a sled net with closing device for investigations of bottom plankton in relation to fish food in the estuaries of the Yenisei and other rivers. In addition, collecting gear, mostly sled nets with or without closing devices, has also been made and used by a number of other workers (Reighard 1894, p. 130; see also Welch 1948, p. 309); Hensen 1895, Beauchamp 1932, Elster 1933, Walford 1938, Werner 1938, Bossanyi 1951, Wickstead 1953, Colman & Segrove 1955; also Hardy & Lucas (at Hull), Beyer (Oslo) and Motoda (Hakodate)—personal communications). The present paper contains the results of a preliminary survey of this fauna as collected with the apparatus previously described by the present author (Bossanyi 1951).

METHODS AND PROCEDURE

This preliminary survey was intended to yield only limited results which could be used as a basis for more detailed work later. It was hoped to gain information on the qualitative composition of the fauna as sampled by the collecting gear used, and some approximate data on the abundance of the various forms. No truly quantitative work was therefore attempted at this stage, such as measuring the volume of water entering the net, or taking replicate hauls. Further since it was found impracticable to take collections at sea at regular intervals for various organizational reasons, the hauls under consideration in the present paper cover the period 1949-52 in an irregular fashion. Most hauls were taken in the summer of 1950 and in the spring and summer of 1952.

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Although collections were made at a number of places in the Blyth area, especially in the initial stages when experimenting with the handling of the gear at sea, the majority were made at two stations, and the results of these only are presented here. The two stations were:

Station 1: Blyth Bay, on sandy bottom approximately $\frac{1}{2}$ mile offshore in a depth of 5-6 fm at mid-tide level;

Station 2: Cambois Bay, north-east of Station 1, on a bottom of fine, compact mud with a small admixture of sand, approximately $1\frac{1}{2}$ miles offshore in a depth of 13-15 fm at mid-tide level. These stations were chosen for the following reasons: two types of bottom material were represented, both sufficiently hard to prevent sinking-in of the gear; at both stations populations of small fish (especially young gadoids) were often present, with which it was hoped to link this study at a later stage; the crew were well acquainted with both grounds so that rocks, wrecks, etc. could be avoided. Further both were near Blyth Harbour which could be quickly reached in an emergency—an important consideration in view of the vessel available at the time for this work. On three occasions, hauls at fairly regular intervals of two or three hours were taken throughout a day: at station 1 in June 1950, and at station 2 in April and July 1952. A projected further such series in the autumn of 1952 at station 2 had unfortunately to be abandoned. All the remaining hauls are individual catches taken on different dates during various daylight hours.

A net of coarse mesh (40 meshes/in.) was used throughout, and all hauls were of 20 min actual towing time. The procedure of shooting, towing and hauling-in the gear was kept as constant as practicable in order to keep the hauls as comparable as possible. The actual method of handling the gear has already been described (Bossanyi 1951). For some hauls at station 2 the gear was provided with a tickler chain as an experiment to determine whether more bottom-living forms would then be caught, but no appreciable differences could be demonstrated in the catches obtained. This may have been due to the chain being too light to disturb the organisms burrowing in the compact bottom on which it was used.

During the two 24-hour series at station 2, simultaneous hauls with two ordinary conical plankton nets (mouth diameter 18 in, one 28 the other 129 meshes/in.) towed 1-2 fm below the surface were made. With these it was hoped to make a rough comparison between the sequence of events at the bottom and that higher up towards the surface. All catches were bottled on deck and immediately preserved with neutral formalin for later examination in the laboratory.

In the laboratory, each catch was first passed through a sieve of 2·5 mm square mesh to separate off the larger forms, the remainder then being subsampled using the method described by Russell (1925, pp. 775-7) and Russell & Colman (1931, pp. 23-5). The subsample was usually one-tenth of the total except when the catch was so rich that smaller proportions had to be taken, in some cases one-hundredth. All the larger forms of each catch were counted and identified, except in a few instances when they were sufficiently abundant also to require subsampling.

Subsamples were examined in detail under the binocular microscope, and all the contained organisms counted. Whenever possible every individual was identified down to species level, but some had to remain lumped together in groups. This occurred when the identity was in any case uncertain, as with some larval forms, or when the organisms belonged to a group with which the author was insufficiently familiar and would have involved a considerable and unjustified added expenditure of time. In practice, nearly all Crustacea (constituting by far the greatest part of the material) were identified to species level, as were some others such as medusae, chaetognaths, etc., and the sex was determined where possible. Whether or not females were carrying eggs was also noted, and juveniles were counted separately from adults, especially in Copepoda. The larvae of Polychaeta, Gastropoda, Lamellibranchiata and Echinodermata, as well as a few other forms such as fish eggs, were lumped together in most cases. *Calanus finmarchicus* (Gunn.) was not separated into its two forms (Rees 1949) beyond noting that both did appear to be present in the material. Species with more than thirty individuals per subsample were counted in one subsample only; sparser forms were however counted in up to three subsamples of a catch and the results averaged in order to reduce the error in estimating total numbers in the whole catch by multiplication. Russell's subsampling method gives an error of not more than 15% when twenty or more specimens are present per subsample. On this basis the figure of 30 was taken as sufficient to enable only one subsample to be counted to obtain the approximate indication of abundance required for this survey. Similarly for the sparser forms, three subsamples counted were considered sufficient to give the approximate degree of abundance of the species in question, although statistically this is doubtless inadequate. The catches were thus treated to some extent as though they were quantitative, although in fact they were at most only roughly comparable. Counts were made to be able to express abundance in terms of round figures of less than 10, tens, hundreds, thousands, etc., of individuals of each species per catch.

The results of the survey are limited by two unavoidable shortcomings. These are the fact that the catches were not taken systematically at regular intervals throughout the year or greater part of the year, and that the gear, like all collecting apparatus, is certainly selective to some degree. The composition of the catches must therefore differ to some extent from that of the actual population in the sea. Furthermore the degree of this difference remains an unknown quantity in the absence of other gear for collecting among the same population and so establishing some comparison. All results must therefore be interpreted with appropriate caution in view of these shortcomings.

RESULTS

The full data are too extensive to print in detail. They have therefore been deposited in the library of the Dove Marine Laboratory, Cullercoats, where they may be consulted.

Taking all catches at both stations together, some 200 forms were captured, excluding those lumped together in major groupings. The term 'form' here usually means the identified species but also includes a few minor groupings, e.g. Pagurid larvae, which were not separated further.

(*a*) *Station* 1

A total of 116 forms were identified including 32 Amphipoda, 21 Copepoda, 18 Decapoda (mostly in larval or post-larval stages), 10 Cumacea, 6 Mysidacea and 6 Coelenterata (medusae); various further groups contributed a few species or forms each. Of this total, however, only twenty-eight forms ever occurred in appreciable numbers—100 or more individuals per catch. Some of these are truly planktonic forms, others are associated in habit with the sea floor (referred to in this paper as 'bottom dwelling forms'), some occurred mostly in daylight and diminished at night, others were predominantly nocturnal in occurrence in the catches, whilst yet others showed no appreciable difference between day and night. These various features are set out in Table 1.

Table 1. *Station 1 catches; maximum abundance and habits of the commoner forms*

Habits are indicated by the symbols: P, planktonic; B, usually associated with the bottom; N, more abundant at night; D, decreasing in numbers at night; ND, apparently unaffected by day-night changes.

In Tables 1 and 3 the numbers (10^4-10^5 etc.) refer to the total number of individuals of a species per catch, juveniles, adults and both sexes all taken together unless otherwise stated.

10^5 PER CATCH	
Acartia clausi Giesbr.	P D
10^4-10^5 PER CATCH	
Calanus finmarchicus (Gunn.)	P D
Pseudocalanus elongatus (Boeck)	P D
Temora longicornis (O.F.M.)	P D
Acartia longiremis (Lillj.)	P D
Alteutha interrupta (Goodsir)	B D
Balanus balanoides (L.), cyprids	P D
Schistomysis spiritus (Norman)	B
Pseudocuma cercaria G.O. Sars	B N
10^3-10^4 PER CATCH	
Centropages hamatus (Lillj.)	P D
Bathyporeia elegans Watkin	B N
Nototropis falcatus (Metzger)	B N
N. swammerdami (M-Edw.)	B N
Diastylis spp., juv. (*bradyi* Norman, *rathkei* (Krøyer))	B N
Pleurobrachia pileus (O.F.M.)	P ND
Littorina littorea (L), eggs	P D
10^2-10^3 PER CATCH	
Podon leuckarti G.O. Sars	P
Hyperoche medusarum (Krøyer)	P ND
Bathyporeia guilliamsoniana (Bate)	B N
Perioculodes longimanus (B. & W.)	B N
Pontocrates altamarinus (B. & W.)	B N
Crangon vulgaris (Fabr.), larvae	P ND
Carcinus maenas (L), zoeae	P D
Pagurid zoeae	P ND
Eutonina indicans (Romanes)	P ND
Phialidium hemisphericum (L)	P ND
Sarsia tubulosa (M. Sars)	P ND
Sagitta elegans Verrill	P ND
S. setosa J. Müller	P ND
Various fish eggs	P ND

All those species generally living on or near the sea floor were mainly nocturnal in occurrence, with the exception of *Alteutha interrupta* (Goodsir) and *Schistomysis spiritus* (Norman). The former was caught both during daylight and at night, though in the latter case in much reduced numbers. The latter species was only caught sporadically and so figures only in some catches, being absent in the 24-

hour series. Its diurnal behaviour is thus not clear from the present results except in so far as all the catches in which it did figure were taken in daylight. The other bottom dwelling forms were sometimes caught in some numbers in daylight, but this was always the case whenever the bottom net had accidentally scooped up a considerable quantity of bottom sand, as occurred on a few occasions when it had probably run into a sandy ridge. Amongst the copepods, *Centropages hamatus* (Lillj.) exhibited the least diminution at night, declining from thousands to hundreds of individuals per catch as compared to the other copepods which declined from thousands or more to tens or less—*Acartia clausi* Giesbr. from over 100 000 to hundreds.

Of those forms which never occurred in numbers of 100 or more per catch, and often less than 10, some occur more or less persistently in a number of catches and would thus appear to constitute a regular if sparse constituent of the fauna. These include *Beroe cucumis* Fabr., *Themisto* sp., *Pontocrates arenarius* (Bate), *Schistomysis ornata* (G.O. Sars), various Euphausiid furciliae, post-larvae of *Pandalus montagui* Leach and *Pontophilus trispinosus* Hailstone, zoeae of *Galathea* spp., *Munida bamffica* (Pennant) and *Corystes cassivelaunus* (Pennant), *Oikopleura* sp., as well as various polychaete, gastropod and lamellibranch larvae and small, recently metamorphosed ophiuroids. In addition there are a number of sparser forms which although not occurring persistently are reasonably conspicuous by virtue of appearing only in catches taken under certain conditions, especially of darkness. These belong mainly to the Mysidacea, Amphipoda and Cumacea, and appear to show a very sharp occurrence pattern relative to light conditions, occurring in the catches in some cases only during complete darkness and not even at dusk or dawn. Included here are *Gastrosaccus spinifer* (Goës), *Apherusa ovalipes* Norman & Scott, *Hippomedon denticulatus* Bate, *Megaluropus agilis* Hoek, *Neopleustes monocuspis* (G.O. Sars), *Orchomenella nana* (Krøyer), *Scopelocheirus hopei* (Costa), *Synchelidium haplocheles* (Grube), *Westwoodilla hyalina* (Bate), *Bodotria scorpioides* (Montagu), *Diastylis lucifera* (Krøyer), *Diastyloides biplicata* (G.O. Sars), *Iphinoe trispinosa* (Goodsir), breeding adults of *Diastylis bradyi* Norman (including males in full breeding dress). The copepod *Oithona similis* Claus on the other hand occurred more in the daytime. Most other species show no diurnal differences, or occur too spasmodically to give any indication.

The vast majority of Crustacea taken, except cirripedes, euphausiids and decapods, were adults. Some species did however show appreciable numbers of juveniles; in *Calanus finmarchicus*, Diastylis spp. and at times in *Schistomysis spiritus* they constituted the majority. *Acartia clausi*, *Nototropis falcatus* (Metzger) and *N. swammerdami* (M.-Edw.) also exhibited an appreciable proportion of juveniles at times, although the adults were always more numerous. It is of course possible that had a finer meshed net been used, the proportion of juvenile stages in the population might have shown itself to be greater. Females were strikingly more abundant than males in the copepods *Calanus finmarchicus*, *Pseudocalanus elongatus* (Boeck) and *Alteutha interrupta*. Females were also usually dominant numerically in *Evadne nordmanni* Lovén and *Podon leuckarti* G.O. Sars, and were often ovigerous, a condition also found in a high proportion of the females of *Schistomysis spiritus*. In *Temora longicornis* (O.F.M.) the sexes were approximately equal in numbers, whilst males predominated persistently in *Centropages hamatus* and, during the 24-hour series of catches, in *Acartia clausi*. Males predominated in *Bathyporeia elegans* Watkin and *B. guilliamsoniana* Bate, but other Amphipods were variable in this respect. The excess of males over females in all Cumacea caught was almost always well marked, a phenomenon already well known and described by other authors (e.g. Fage 1933) for night-time hauls. This excess did not occur among the isolated individuals caught during daylight. Table 2 gives the actual numbers counted in two night hauls taken in complete darkness for the four abundant species of Amphipods and Cumacea.

Table 2. *Station 1. Numbers of adults of dominant species of Amphipoda and Cumacea taken in two night catches in the 24-hour series, 12 and 13 June 1950*

Catch	*Bathyporeia elegans*		*B. guilliamsoniana*		*Diastylis bradyi*		*Pseudocuma cercaria*	
number	males	females	males	females	males	females	males	females
VII	4268	225	309	21	21	25	13943	5961
VIII	792	62	36	–	87	12	13792	8610

(*b*) *Station* 2

A total of 174 forms were identified including 54 Amphipoda, 24 Copepoda, 21 Decapoda (mostly larval and post-larval stages), 13 Cumacea, 11 Ostracoda, 9 Mysidacea, 8 Isopoda, and 8 Coelenterata (medusae); various further groups a few species or forms each. Of this total, only thirty-five forms ever occurred in appreciable numbers of 100 or more individuals per catch. As in catches at station 1, some of these are truly planktonic, some are associated with the sea floor, some occurred mostly in daylight and diminished in number at night whilst others were predominantly nocturnal or exhibited no appreciable difference in diurnal occurrence in the catches. These features are shown in Table 3.

The Cumacea caught were again predominantly nocturnal in occurrence, whilst *Alteutha interrupta* was caught mostly during daylight in the same way as at station 1. The Ostracoda and Isopoda figuring in Table 3 must be interpreted with caution. It is probable that these were mostly scooped up with bottom material rather than caught whilst swimming above the bottom, although certain of the former, e.g. *Polycope orbicularis* G. O. Sars, are known to spend part of their time swimming over rather than crawling on the bottom (Müller 1894, Elofson 1941, and others) and may have been captured whilst so doing. Amongst the copepods, it is noticeable that *Centropages hamatus* appears to show no difference in occurrence between day and night catches. Of the forms which never occurred in numbers of 100 or more per catch, some were taken fairly persistently in a number of catches and collectively constitute an important proportion of them. Amongst these forms three categories can also be discovered—predominantly nocturnal, predominantly daylight and those exhibiting little diurnal change. These are shown in Table 4.

Other forms caught which do not figure in Tables 3 and 4 occurred in small numbers (<100 individuals per catch) and also were found only sporadically. These included a number of Amphipoda, Cumacea and Mysidacea for instance, predominantly nocturnal in occurrence.

The great majority of all Crustacea taken, except *Calanus finmarchicus*, Cirripedia, *Diastylis* spp., and Decapoda, were adults. Where juvenile stages occurred, as in *Acartia clausi*, they were unimportant in numbers relative to the adults.

Table 3. *Station 2 catches; maximum abundance and habits of the commoner forms*

Symbols for habits as in Table 1.

10^4-10^5 PER CATCH	
Calanus finmarchicus	P D
Pseudocalanus elongatus	P D
Centropages hamatus	P ND
10^3-10^4 PER CATCH	
Temora longicornis	P D
Acartia clausi Giesbrecht	P D
Balanus balanoides, cyprids	P ND
Crangon allmani Kinahan, larvae	P D
Pagurid zoaeae	P D
Sagitta elegans	P D
10^2-10^3 PER CATCH	
Acartia longiremis	P D
Alteutha interrupta	B D
Evadne nordmanni Lovén	P D
Balanus balanoides nauplii	P ND
Verruca strömii (O.F.M.), nauplii	P ND
**Bythocythere turgida* G.O. Sars	B
**Cythereis jonesi* (Baird)	B
**C. tuberculata* G.O. Sars	B
**Cytheropteron latissimum* (Norman)	B
**Polycope orbicularis* G.O. Sars	B
**Pleurogonium inerme* G.O. Sars	B
**P. rubicundum* G.O. Sars	B
Nyctiphanes couchi (Bell), furcilias	P D
Thysanoessa inermis (Krøyer), furcilias	P D
Diastylis spp., juv. (*bradyi, rathkei*)	B N
Pseudocuma cercaria	B N
Crangon vulgaris, larvae	P D
Pandalus montagui Leach, larvae and post-larvae	B ND
Galathea spp, zoaeae	P D
Carcinus maenas, zoaeae	P D
Pleurobrachia pileus	P ND
Sagitta setosa	P D
Aphroditid larvae	P
Pectinaria sp., larvae	P
Oikopleura sp.	P ND

* Probably scooped up with bottom material.

Females predominated in the copepods *Temora longicornis, Acartia clausi* and *Pseudocalanus elongatus*, whilst the sexes were approximately equal in numbers in *Centropages hamatus*. The ratio was variable in Amphipoda generally, but males predominated again in the Cumacea.

(c) *Comparisons*

The catches obtained in April and July at station 2 show appreciable differences in their species composition. Thus forty-seven species or forms caught in April do not occur in July catches, and fifty-nine taken in July do not figure in the April catches. Many of these are doubtless chance differences, but some species among them are conspicuously present or absent in one or other series of catches. Furthermore among those which were taken at both times, certain species are distinctly more abundant in one month than in the other. Table 5 summarizes these features. Those forms occurring more abundantly in April tend to be bottom dwellers, whilst those more abundant in July tend to be planktonic forms as might be expected considering the increased abundance and variety of zooplankton which always develops as the summer advances.

It is probable that the greater number of species captured at station 2 (especially noteworthy in the Amphipoda) is attributable to three causes: somewhat more hauls were taken there than at station 1, and many of them in a different season and also in a different year; more bottom material tended to be scooped up at station 2, especially during the July 1952 24-hour series, which would account for several species of Ostracoda, Isopoda and certain Amphipoda being caught; there is a greater variety of species living on the muddy bottom at the depth of station 2 than under the conditions obtaining at station 1.

Table 4. *Station 2 catches; occurrence of the less common forms*

A, present predominantly or entirely in April; J, Present predominantly or entirely in July; AJ, present indifferently in both April and July; N, more abundant at night; D, decreasing in numbers at night; ND, unaffected by day-night changes.

Oithona similis Claus	J	ND
Longipedia coronata Claus	A	ND
Amphilochoides serratipes (Norman)	AJ	ND
Bathyporeia elegans Watkin	A	N
Dulichia falcata (Bate)	A	ND
Hippomedon denticulatus (Bate)	AJ	N
Melita obtusata (Montagu)	AJ	N
Melphidippella macra (Norman)	J	ND
Metopa rubrovittata G.O. Sars	A	ND
Nototropis falcatus (Metzger)	A	N
N. swammerdami (M-Edw.)	A	D
Perioculodes longimanus (B. & W.)	A	N
Tryphosites longpipes (B. & W.)	AJ	N
Westwoodilla hyalina (Bate)	AJ	N
Themisto sp.	A	ND
Schistomysis ornata (G.O. Sars)	AJ	ND
Eudorella truncatula Bate	AJ	N
Euderellopsis deformis (Krøyer)	A	ND
Corystes cassivelaunus (Pennant), zoaeae	AJ	ND
Autolytus prolifer (O.F.M.)	AJ	D
Gastropod larvae	A	ND
Lamellibranch larvae	AJ	ND
Ophiuroids, young, recently metamorphosed	AJ	ND

A majority of those forms caught at station 2 and not at station 1 were bottom dwellers and not planktonic in habit. Of the approximately ninety forms in question, some fifty would be expected to occur at station 2 from their known distribution pattern (substratum and depth preferences), and all but a few of these are Ostracoda, Isopoda, Amphipoda and Cumacea. This observation underlines the importance of the third reason given above. Among the remaining forms the greater part were caught at station 2 only probably by chance and could just as well have occurred at station 1 as far as can be seen from their known distribution pattern. Most of these are planktonic in habit, e.g. *Paracalanus parvus* (Claus), decapod larvae, some Mysids, larvae of other benthonic adults and medusae. Only a small proportion were amphipods and other bottom dwellers.

At station 1 some thirty forms were found which were not taken at station 2, eighteen of them probably by chance only, but twelve undoubtedly characteristic of the conditions obtaining in Blyth Bay. These latter included such littoral forms as the copepods *Parapontella brevicornis* (Lubbock), *Acartia discaudata* (Giesbr.), *Harpacticus chelifer* (O.F.M.) and *Thalestris longimana* Claus, as well as the amphipod *Gammarellus homari* (Fabr.), and forms which are largely characteristic of shallow water and sandy bottoms such as the amphipods *Bathyporeia guilliamsoniana*, *Megaluropus agilis*, *Pontocrates arenarius* and the cumaceans *Iphinoe trispinosa* and *Pseudocuma similis* G.O. Sars.

Other species, although caught at both stations, were much more abundant at one than at the other. Thus the planktonic forms *Acartia clausi* and *A. longiremis* (Lillj.), *Pleurobrachia pileus* (O.F.M.), *Eutonina indicans* (Romanes) and *Hyperoche medusarum* (Krøyer) were more abundant in Blyth Bay than further off in Cambois Bay. This has often though not always been found to be the case in general plankton collections in the area, and may be due to some littoral and estuarine effects—except doubtless in *Hyperoche medusarum* which occurs with associated medusae. Amongst bottom dwellers certain species were found more in Blyth Bay in conformity with their usual distribution pattern on littoral or shallow

Table 5. *Station 2 : forms showing marked seasonal difference in occurrence*

P, planktonic habit; B, generally associated with the bottom in habit; S, probably scooped up with bottom material, not swimming.

PRESENT IN APRIL, ABSENT IN JULY:	
Amphipoda:	
Bathyporeia elegans Watkin	B
Metopa alderi (Bate)	B
Nototropis falcatus (Metzger)	B
Cumacea:	
Diastylis bradyi Norman	B
Euderellopsis deformis (Krøyer)	B
Gastropoda:	
Miscellaneous larvae	P
MORE ABUNDANT IN APRIL:	
Copepoda:	
Longipedia coronata Claus	B
Cirripedia:	
Verruca strömii (O.F.M.) nauplii	P
Amphipoda:	
Themisto sp.	P
Dulichia falcata (Bate)	B
Harpinia serrata G.O. Sars	B
Hippomedon denticulatus (Bate)	B
Metopa rubrovittata G.O. Sars	B
Nototropis swammerdami (M-Edw.)	B
Perioculodes longimanus (B. & W.)	B
Mysidacea:	
Schistomysis ornata (G.O. Sars)	B
Cumacea:	
Diastylis spp., juv.	B
Pseudocuma cercaria G.O. Sars	B

PRESENT IN JULY, ABSENT IN APRIL:	
Copepoda:	
Oithona similis Claus	P
Cladocera:	
Evadne nordmanni Lovén	P
Ostracoda:	
Bythocythere turgida G.O. Sars	S
Polycope orbicularis G.O. Sars	S
Mysidacea:	
Mysidopsis didelphys Norman	B
Cumacea:	
Diastyloides biplicata (G.O. Sars)	B
Decapoda:	
Pandalus montagui Leach	B
Ctenophora:	
Pleurobrachia pileus (O.F.M.)	P
Coelenterata:	
Euphysa aurata Forbes	P
Echinodermata:	
Various plutei	P
MORE ABUNDANT IN JULY:	
Ostracoda:	
Cythereis jonesi (Baird)	S
Cytheropteron latissimum (Norman)	S
Amphipoda:	
Melphidippella macra (Norman)	B
Decapoda:	
Pagurid zoeae	P
Galathea spp., zoeae	P
Carcinus maenas (L.), zoeae	P
Chaetognatha:	
Sagitta elegans Verrill	P
Polychaeta:	
Aphroditid larvae	P
Various other larvae	P

sandy bottoms, e.g. *Alteutha interrupta* (which at station 2 is probably nearing its depth limit), *Bathyporeia elegans*, *Nototropis falcatus* and *N. swammerdami*, *Pontocrates altamarinus* (B. & W.), *Synchelidium haplocheles*, *Schistomysis spiritus*, *Diastylis bradyi* and *Pseudocuma cercaria* G.O. Sars. Similarly other bottom dwellers were more in evidence on the muddy ground in deeper water at station 2 in conformity with their usual distribution, e.g. *Longipedia coronata* Claus, *Cythereis tuberculata* G.O. Sars, *Amphilochoides serratipes* (Norman), *Melphidippella macra* (Norman), *Metopa rubrovittata* G.O. Sars, and larvae and post-larvae of *Crangon allmani* Kinahan and *Pandalus montagui*.

DISCUSSION

The general picture emerging from the results described above presents some interesting indications, but the evidence from the present survey is insufficient to generalize these, and more work along some of the lines suggested by the present results is required. At station 1 in Blyth Bay in the daytime, the 'bottom plankton' was in effect largely ordinary plankton, dominated by a few species of Copepoda amongst which *Arcartia clausi* was the most conspicuous by its numbers. This plankton contained a substantial proportion at most times, or in some cases, at certain times, of such forms as *Pleurobrachia pileus*, a few medusae (especially *Eutonina indicans*, *Sarsia tubulosa* (M. Sars) and spp.), *Sagitta elegans* Verrill, larvae of *Balanus balanoides* (L.), Cladocera (in this case *Podon leuckarti*), hyperiid Amphipoda especially *Hyperoche medusarum* associated with the medusae, occasional large swarms of *Schistomysis spiritus*, various decapod larvae, fish eggs, larvae of Polychaeta, Mollusca and fish. In addition to these, however, there were indications of the proximity of the bottom in the presence of some organisms associated with the sea floor. Amongst these *Alteutha interrupta* and newly metamorphosed ophiuroids were especially noticeable, as well as occasional *Nototropis swammerdami*, *Pseudocuma cercaria* and other amphipods and cumaceans. A few of these may, however, have been scooped up with bottom material in some cases.

During the hours of darkness, a profound change took place in the composition of the 'bottom plankton'. The copepods diminished in numbers near the bottom and lost their dominant position, whilst a considerable variety of Amphipoda and Cumacea appeared and now dominated the swimming fauna there. Other planktonic forms seemed to remain largely the same, e.g. the decapod larvae as a whole, ctenophores, medusae and their associated hyperiids.

Amongst the amphipods and cumaceans only a few species were conspicuously abundant and it is these which in effect dominated the nocturnal 'bottom plankton'. These were *Bathyporeia elegans* and *B. guilliamsoniana*, *Nototropis falcatus* and *N. swammerdami*, *Pseudocuma cercaria* and *Diastylis* spp. (juveniles and adults of *D. bradyi* and *D. rathkei* (Krøyer) var.), together with *Pontocrates altamarinus* and *Perioculodes longimanus* (B. & W.) to a lesser degree. Some other species whilst not so abundant numerically were large and conspicuous forms, and may have contributed substantially to the biomass of the nocturnal 'bottom plankton'. Examples of these were *Hippomedon denticulatus* and *Iphinoe trispinosa* amongst others. A number of the nocturnal forms were caught only when it was quite dark, thus apparently showing a very sharp behaviour relative to light, but more catches are necessary to confirm this behaviour pattern.

Little can be said regarding seasonal differences at station 1 as the period covered by catches there was too short. The only differences within this period were the well-known ones usually observed in the plankton as the summer advances, such as a decrease in cirripede larvae and an increase in decapod larvae, Ctenophora and medusae.

At station 2 in Cambois Bay, the variety of species taken was greater than at station 1, especially in bottom dwelling forms. Total numbers tended to be rather less, however, except in most Copepoda. The great nocturnal swarms of a few species of Amphipoda and Cumacea were absent although the general pattern of diurnal change was similar. There was thus a daytime plankton dominated by Copepoda with a varying proportion of Cladocera, cirripede larvae, decapod larvae, Ctenophora and medusae. The night catches still contained some of these though in diminished numbers, whilst a variety of Amphipoda and Cumacea took on the major role. Unlike the situation at station 1, *Sagitta elegans* tended to diminish in numbers at night, but *Centropages hamatus* appeared to remain unaffected.

Seasonal differences at station 2 were quite marked when comparing the results of the April and July 24-hour series. In April, although there was an increase of Amphipoda and Cumacea at night, quite a number of these were also caught during daylight, so that daytime and night-time catches were not so sharply differentiated. In July, however, the distinction between them was much sharper and similar to that found at station 1 in June, with the amphipod and cumacean fauna as a whole distinctly caught only at night. The reasons for this striking difference between April and July catches at the one station can only be surmised at this stage as the present survey yields no further evidence, but three suggestions may be put forward. In April the sunlight is less intense and the position of the sun is above the critical angle for a shorter period per day than in July; in addition the water is likely to be more turbid then. Day and night conditions of illumination near the bottom at the depth of station 2 may therefore not be sharply differentiated during April but become increasingly so as the summer advances. Secondly a number of authors (e.g. Foxon 1936, Tattersall 1938, Watkin 1939) have suggested that the upward migration of the bottom dwelling forms may have a reproductive and not a feeding significance. It is therefore possible that this upward movement at night becomes more marked as the summer and sexual maturity of an increasing proportion of organisms in the fauna advances. Thirdly different species doubtless have different reactions to day and night conditions, and as the species composition of the nocturnal fauna in April and July is considerably different, such differences in behaviour will make themselves felt in the behaviour of the fauna as a whole and so in the catches obtained. The planktonic Copepoda caught appeared to show little difference in their diurnal behaviour between April and July; a diminution in numbers near the sea floor at night occurred at both times.

Considering the difference in species composition of the fauna caught in April and July, the main features of which are summarized in Table 5, it is curious that a number of the bottom dwelling forms which were conspicuously more in evidence in April or even altogether absent in the July catches were generally those forms more characteristic of shallow water and sandy bottom. They were in fact those species which constituted the bulk of the nocturnal fauna at station 1—*Bathyporeia elegans*, *Nototropis falcatus*, *N. swammerdami*, *Perioculodes longimanus*, *Hippomedon denticulatus*, *Diastylis bradyi* and *Diastylis* spp. juv., and *Pseudocuma cercaria*. This observation raises the question of the possibility that these forms migrate further offshore during the winter into somewhat deeper water and return to the sandy shallow areas during spring and summer. This suggestion is at present a mere speculation without further evidence from the present survey. It is interesting to note in this connection, however, that the sandy beaches above and below low water mark in the area investigated undergo considerable shifting at times, especially during periods of stormy weather. Local beaches then tend to become denuded of sand, only to regain it later, whilst during inshore fishing operations, *e.g.* in Blyth Bay itself, with beam trawls and other gear, obstacles on the bottom occasionally foul the nets hauled over a stretch of ground where at other times no such trouble is experienced. Such considerable shifting of the substratum must have marked effects on the fauna inhabiting it.

It should be emphasized that the above species which constituted the nocturnal swarms in Blyth Bay, although present in Cambois Bay in April, did not produce such swarms there. They added to the variety of the amphipod and cumacean fauna there, but did not dominate the night bottom plankton. Such large numbers of a few species as were found in Blyth Bay were in fact absent at the Cambois station and there was no evidence of other species replacing them in this respect, either in April or July. Thus the Cambois station showed a greater variety of forms but far fewer total numbers of them.

The daylight bottom plankton over the two stations was largely similar except for the two Acartia species, *Pleurobrachia pileus* and *Eutonina indicans* already mentioned.

The catches made with the two ordinary plankton nets near the surface in the April and July Cambois series are not comparable with those made with the bottom net because of their different size and mesh-size. They are, however, comparable with each other, and it was hoped to compare the diurnal changes in the bottom net catches with parallel changes in the catches nearer the surface. Such changes near the surface were in fact found, especially in the April series. Thus there was a definite tendency for the copepods *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Temora longicornis* to increase near the surface at night, corresponding with the decrease already noted in the bottom net catches taken at about the same time. The same is again apparent for *Calanus finmarchicus* in the July series, but the other species are inconclusive. These results, even though very approximate, nevertheless tend to fit the expected pattern.

A few species of bottom dwelling forms were also caught in the ordinary plankton nets near the surface, but in no case more than ten individuals per catch—mostly only one or two. These species were in April, at night only, *Bathyporeia elegans*, *Westwoodilla hyalina*, *Nototropis vedlomensis* (B. & W.), *Amphilochus neapolitanus* della Valle, *Diastylis bradyi*, *D. rathkei* var., *Pseudocuma cercaria*; daytime and night, *Metopa alderi* (Bate), *M. spectabilis* G. O. Sars; daytime only (once), *M. rubrovittata*. In July there were, at night only, *Ampelisca spinipes* Boeck, *Argissa hamatipes* (Norman), *Melphidippella macra*, *Megamphopus cornutus* Norman, *Nototropis swammerdami*, *Perioculodes longimanus*, *Bodotria scorpioides*, *Diastylis bradyi*. These results would indicate that bottom dwelling forms reach upper layers during the night and, earlier in the year, to some extent also in the daytime. But they did so in small numbers quite out of proportion to the numbers found swimming just above the bottom at night. This does not of course exclude the possibility of large numbers reaching the surface, but no such swarms were encountered in the present survey.

The broad conclusion indicated by this survey is that at the two stations investigated and at the time the catches were made, the daylight bottom plankton in immediate proximity to the sea floor was fairly similar and was in effect largely ordinary plankton with a small admixture of bottom dwelling forms at times, especially at the Cambois station in the earlier part of the year. Differences in daylight bottom plankton at the two stations were in the abundance of such forms as *Acartia clausi* and the occurrence, even if only in small numbers, of strictly littoral forms in Blyth Bay. The night bottom plankton at the two stations, however, differed greatly both qualitatively and quantitatively: it was in effect a function of, and closely related to, the nature of the bottom and the depth of water. It further appeared to vary seasonally both in qualitative composition and in behaviour with regard to day and night conditions.

No data are available from the present survey on the biomass of the bottom plankton and its changes, but the diurnal changes of this plankton indicate that there may be considerable variations in this between day and night. In Blyth Bay, where very large numbers of comparatively large forms dominate the nocturnal bottom plankton, the biomass may be considerably greater at night than in the daytime, and may thus increase the food supply of certain predators. The large individual size of night planktonts, especially Amphipoda and Cumacea, also brings this plankton within the range of predators which hunt their prey singly, thus providing, at least in theory, better feeding conditions at night. This may be of great importance for young fish, e.g. small gadoids (cod, whiting, coal-fish) which often occur in large numbers in Blyth Bay during the summer. Most Teleosts are, however, believed to hunt their prey by sight and therefore probably only by day, and so may not in fact have access to these fertile nocturnal pastures. Yet the extent to which this is in fact true in nature still appears to be uncertain, and until further work provides more evidence in this sphere the possibility of night feeding cannot be ignored. Investigations along these lines have been begun in the Blyth area.

Benthonic filter feeders constitute another group of organisms whose feeding may be considerably influenced by changes in the bottom plankton. Such feeders collect much detritus for food but doubtless depend partially on living planktonts of small size, such as small copepods and their juvenile stages, etc., which would appear to be more abundant within their reach in the daytime. This aspect of bottom plankton ecology also requires further investigation using finer-meshed nets than the one so far employed.

Again, the importance of the large numbers of Ctenophora such as *Pleurobrachia pileus* which appear seasonally in the plankton, requires further work. These forms are known to cause tremendous havoc amongst the planktonic community and may at times decimate it. In the present survey, this ctenophore was found in large numbers in the bottom net catches in Blyth Bay both during the day and at night. Most of those taken during darkness were observed to have eaten amphipods and cumaceans which were discovered either wholly or partially swallowed. Digestion in ctenophores is known to be very rapid (Hyman 1940, p. 690) so that the food is not recognizable for long in the pharynx, and a considerable proportion of these *Pleurobrachia* had undoubtedly captured their prey when already themselves caught in the net. Nevertheless it remains highly probable that *P. pileus* took a considerable toll of the nocturnal fauna swimming near the sea floor, and its effect on the bottom dwelling populations of such species as *Bathyporeia* spp., *Nototropis* spp., *Diastylis* spp., and *Pseudocuma cercaria* inhabiting Blyth Bay must be appreciable.

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SUMMARY

1. The 'bottom plankton' at two stations of differing depth and type of bottom was surveyed with a bottom sled net by day and night.
2. The small natant fauna just above the sea floor is rich both by day and at night.
3. The daytime plankton at both stations consisted mainly of ordinary plankton dominated by a few species of Copepoda but contained a small proportion of bottom dwelling forms, especially earlier in the year at the deeper station.

4. The nocturnal plankton differed considerably at the two stations. Its composition was related to the depth and nature of the sea floor since it was dominated by bottom dwelling Amphipoda and Cumacea. More variety was found over mud, but larger numbers over sand.

5. The bottom dwelling forms showed different diurnal behaviour in April and July, for which reasons are suggested.

6. The food relationships of 'bottom plankton' are discussed.

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THE FOOD OF THE DEMERSAL FISH OF A WEST AFRICAN ESTUARY

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(With 4 Figures in the Text)

As part of a project to investigate the relationship between the West African demersal fish and the marine benthic communities, an analysis of the food and feeding intensity of the fish commonly taken in otter-trawls in the Sierra Leone River was undertaken by this Institute in 1952. A quantitative survey of the benthos, and a study of its community structure, is now nearing completion in the same area.

The study of the food of demersal fish was confined by practical considerations to the Sierra Leone River, which is convenient to these laboratories and calm enough to be worked at all seasons by the open launches used in the period 1952-55. The term 'Sierra Leone River' is applied to the large and open estuary of the Rokel River; at the mouth, between Cape Sierra Leone and the Bullom Shore, it is almost ten miles wide. Into this estuary flow the effluents of the Rokel River, of several smaller rivers, and of innumerable serpentine creeks draining mangrove flats. There is no bar across the mouth, and the main channel is 10-12 fm deep, so that there is free influx of marine organisms. From May to October, during the rainy season, conditions of lowered salinity extend right to the mouth, while during the dry season there is a considerable inflowing of sea water. The tidal streams are strong, reaching 5 kn on the ebb of springs, and much transport of deposits occurs, so that the nature of the bottom at any one place may change radically over a period of only a few months.

Demersal fish, of which the majority are euryhaline, are present in the estuary throughout the year and are much fished from canoes with hand and long-lines.

MATERIAL

During the three years April 1952 to March 1955 the Institute's launches have carried out a standard trawling programme in the Sierra Leone River at frequent intervals, usually each week. Six hauls, each of one hour's duration and starting at the same state of the tide, were made over a standard course in the mid-estuarine region on each occasion. Otter-trawls with 30-ft headlines, and a mesh of 3 in. in the cod-end were used.

Besides the ichthyometric data, general observations were made on the food organisms which could be recognized in the stomach of each fish taken; in this way, more than 20,000 specimens of twenty-five species of fish were examined, and eight of these species are represented by more than 1000 examinations. This data, entered on the record sheets of the standard trawl, furnished the bulk of the material available to me. It must be emphasized that these examinations were undertaken at sea under difficult conditions, and that relatively few stomachs were preserved for further analysis until the final year of the programme; the results were not intended to be of other than a general nature, and specific or generic determinations were rarely made.

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After October 1954 all the stomach contents were preserved and brought into the laboratories in order to identify as precisely as possible the food organisms taken by each species rather than to measure the intake of each fish, and so for convenience the stomach contents of each species were bulked. Trawling was also carried out in other parts of the estuary, and the results of these trips are included in the data for the identification of the food organisms.

The relative importance of each type of food in the diet of a species of fish may be determined either by measuring the relative weights or volumes of each food contained in the stomachs or by determining the percentage of food-containing stomachs in which the type of food in question occurs. Jones (1954) has shown that in *Gadus merlangus* there is a fairly close correlation between results obtained by both methods, the curves of percentage occurrence corresponding very well with those of percentage weight for each type of food. The correlation is disturbed when there is a high percentage occurrence of very small crustacea, or other forms with negligible weight. The quantitative analysis in the present work was restricted, from the nature of the data, to the percentage occurrence method and all the percentages that are quoted later in the paper are the percentages of those stomachs containing food that contain the particular food under discussion; the total of such percentage occurrences frequently reaches a number much in excess of 100 for a species, for each stomach may contain more than one type of food.

The intensity of feeding can be measured by a similar method; an analysis using the percentage occurrence of empty stomachs has been shown by Jones to give very similar results to one based on the weight of food in the stomachs. In the present investigations only the former method was possible.

RESULTS

The food of most of the demersal fish is derived from the invertebrate benthos, and from actively moving invertebrates and fish which remain near the bed of the estuary. Forms such as the mullets (*Mugil, Liza*) which feed upon the microflora of the bottom, normally frequent the shallower reaches of the estuary, and so are taken only rarely in the trawl. A number of pelagic fish occurred fairly regularly in the trawl catches, but these are outside the scope of the present work and draw their food from the zooplankton and phytoplankton, or are ichthyophagous.

The demersal fish may be arranged into three groups according to the nature of their diet, and such an arrangement is used in Table 1. The first group consists of the few species which are specialized fish eaters, although it will be seen from the table that the diet of most of these may include a small proportion of actively

Table 1. *The percentage occurrence of the various types of food for each species of fish*

The data are derived from the records of the standard trawling programme. The arrangement of the fish is according to the nature of their diet, with the exception of the last two species, whose food is too miscellaneous to categorize.

	Total	% empty	No. with food	Penaeids	Brachyura	Mysids	Cumacea	Cirripedea	Stomatopoda	Amphipoda	*Callianassa*	Pagurids	Polychaeta	Gastropoda	Lamellibranchiata	Cephalopoda	Ophiuroidea	Asteroidea	*Rotula*	Holothuroidea	*Lingula parva*	Fish	Fish Eggs	Fish Larvae	Detritus
ICHTHYOPHAGOUS																									
Pristis spp.	5	2·0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3·0	–	–	–
Pteroplatea micrura	38	47·5	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	100·0	–	–	–
Pseudotolithus senegalla	1 043	55·1	468	16·9	2·2	–	–	–	3·0	–	–	–	0·6	–	–	0·2	–	–	–	–	–	75·0	–	0·7	–
Psettodes belcheri	11	7·0	–	–	–	–	–	–	–	–	–	–	–	–	–	1·0	–	–	–	–	–	2·0	–	–	–
ACTIVE EPIFAUNA AND FISH																									
Rhinobatus rasus	6	–	–	3·0	1·0	–	–	–	1·0	–	–	–	–	–	–	–	–	–	–	–	–	2·0	–	–	–
Arius latiscutatus	472	39·8	284	28·5	26·7	–	–	–	1·4	–	0·3	0·2	41·5	–	1·4	–	2·1	–	–	–	–	33·0	–	–	5·9
Lutjanus modestus	2	–	–	–	2·0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scyris alexandrinus	10	3·0	–	4·0	–	1·0	–	–	2·0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1·0	–
Diagramma macrolepis	327	29·6	230	40·0	61·7	0·4	–	–	0·8	–	–	–	6·7	0·4	1·3	–	0·7	–	–	–	–	3·0	–	–	1·3
Pseudotolithus elongatus	3 291	53·8	1 772	23·0	5·2	36·8	1·3	–	0·8	–	–	–	5·4	–	–	0·12	–	–	0·6	–	0·24	24·6	–	–	8·4
Pinnacorvina epipercus	67	35·8	43	28·0	83·5	–	–	–	13·8	–	3·6	–	4·6	–	–	–	2·3	–	–	–	–	–	–	–	–
Pseudotolithus senegalensis	142	43·6	80	44·5	6·3	–	–	–	25·0	–	–	–	–	–	–	–	–	–	–	–	–	32·5	–	–	–
Polydactylus quadrifilis	341	24·8	260	50·0	13·1	–	–	–	18·5	–	–	–	0·4	–	–	12·2	–	–	–	–	–	34·6	–	–	–
SEDENTARY EPIFAUNA AND INFAUNA																									
Trygon margarita	2 375	24·2	1 798	13·0	11·9	0·6	–	–	0·9	–	1·3	–	78·3	–	2·1	0·05	0·5	–	0·05	0·05	0·2	0·3	–	–	0·15
Pomadasys jubelini	4 176	49·2	2 121	2·9	2·4	–	0·04	–	1·1	–	0·8	–	75·3	–	1·2	–	4·8	–	5·6	–	5·1	2·0	–	–	3·3
Monodactylus sebae	59	35·6	38	2·6	–	7·9	–	–	–	–	–	–	84·2	–	–	–	–	–	–	–	–	23·6	–	–	–
Drepane punctata	3 840	17·9	691	2·0	0·05	0·3	0·6	–	0·1	–	–	–	86·4	–	0·2	–	2·8	–	0·2	–	4·0	0·1	–	–	8·4
Chaetodipterus lippei	1 047	31·2	720	0·8	0·1	–	–	–	–	–	–	–	31·2	–	0·3	–	1·8	–	0·3	–	0·1	–	0·3	–	66·9
Gerres melanopterus	10	5·0	–	–	–	–	–	–	–	–	–	–	3·0	–	–	–	–	–	–	–	1·0	–	–	–	1·0
Galeoides decadactylus	1 437	39·0	876	25·1	10·5	0·4	–	–	5·4	–	0·4	–	22·4	–	1·1	–	6·8	–	1·1	–	2·0	3·0	–	–	31·0
Synaptura punctatissima	23	19·0	–	–	–	–	–	–	–	–	–	–	4·0	–	–	–	–	–	–	–	–	1·0	–	–	–
Cynoglossus goreensis	1 681	39·9	60	11·1	22·2	–	–	–	8·4	–	2·2	–	31·8	–	3·7	–	0·4	–	1·9	–	25·7	1·6	–	–	11·4
Lagocephalus laevigatus	2	–	–	–	–	–	–	–	–	–	–	–	–	–	2·0	–	–	–	–	–	–	–	–	–	–
Hemiconiatus guttifer	59	30·5	41	–	4·8	–	–	9·7	–	–	–	–	2·4	2·4	58·4	–	-	4·8	7·2	–	–	2·4	–	–	–
Pteromylaeus bovina	7	1·0	–	1·0	1·0	–	–	–	–	–	1·0	–	2·0	–	–	–	–	–	–	–	–	1·0	–	–	–
Otoperca aurita	16	6·0	–	–	–	–	–	–	–	–	–	–	1·0	–	–	–	–	–	–	–	–	1·0	–	–	8·0

swimming invertebrates, such as penaeid prawns and small squids. The second group includes those fish which feed mainly on the more active members of the epifauna, and which are ichthyophagous only to a limited extent. These may be considered together with the previous group as fish which feed as active predators upon the animals which move over, or on, the bottom. The last group comprises those species which browse on the infauna of the benthos—though they must need a great deal of alertness and speed since they feed on polychaetes and burrowing crustacea which are able to retreat very swiftly into their burrows. Polychaetes form the bulk of the diet of the more typical members of this group, together with some brachiopods, lamellibranchs and crustaceans.

The food of each species is discussed individually below; the arrangement of the species is systematic, rather than according to the diet.

PRISTIDAE

1. *Pristis* spp. The only food found in the five stomachs of this genus which were available consisted of unidentifiable remains of fish.

RHINOBATIDAE

2. *Rhinobatus rasus* Garman 1908 (Guitarfish). Monod (1927) found decapod crustacea and young *Ethmalosa dorsalis* in the food of this species which he examined in the Cameroons. The contents of the six stomachs which were examined in the present work also indicate that the diet is based upon Crustacea and fish.

TRYGONIDAE

3. *Pteroplatea micrura* Schneider 1801 (Batskate). Of the thirty-eight specimens examined, twenty were found to contain remains of fish while the remainder were empty; this would appear to indicate an exclusively ichthyophagous diet, at least in this area.

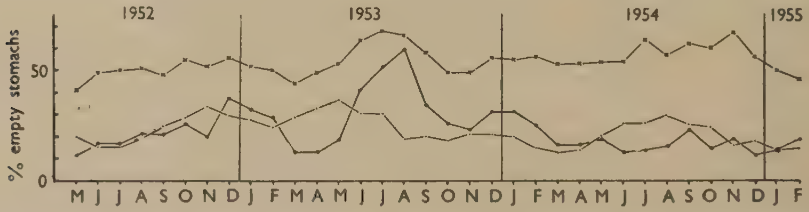

Fig. 1. The percentages of empty stomachs from the results of the standard trawling programme for three species of fish feeding on the benthic infauna; three-period running means. X-X-X *Pomadasys jubelini*; ●-●-● *Drepane punctata*; ·—·— *Trygon margarita*.

4. *Trygon margarita* Gunther 1870 (Stingray). This species takes the bulk of its food from the infauna of the benthos, and polychaetes occur in between 50% and 100% of those stomachs containing food (Table 1). Smaller, but fairly regular, percentages of crustacea occur and these are mainly penaeid prawns and small crabs. No regular seasonal variation can be detected in either the feeding intensity (Fig. 1) or in the composition of the diet, from the monthly analyses of the results of the standard trawling programme.

The identification of the bulked stomach contents is in good agreement with the percentage occurrence given in Table 1, and shows that many of the crustacea eaten are burrowing forms—Stomatopoda, Thallassanidea, Tanaidacea and *Alpheus*, and that the crabs taken are procellanids which live to a great extent below stones, and in crevices. The species of polychaetes taken are similar to those found in the diets of other polychaete-feeding fish; the relative importance of these and other food organisms is given in Table 2. Ophiuroids are relatively common in the stomach contents, especially *Amphioplus congensis* which lives buried in soft mud with only the tips of the arms above the surface of the deposit; the presence of a number of gephyreans, typical of similar situations, should also be noted.

The dependence of *Trygon* on the infauna of soft deposits in West African estuaries has already been noted by Monod (1927) who examined the stomach contents of two specimens in the Cameroons and found such organisms as *Callinectes*, various isopods and *Rhopalodina lageniformis*; the latter species is restricted in the Sierra Leone River to deposits of fairly soft mud.

Table 2. *Food organisms identified in the diet of* Trygon margarita, *with the numbers occurring in the material examined*

POLYCHAETA		CRUSTACEA	
Clymene monilis	16	*Squilla africana*	34
Pectinaria sourei	11	*Latreutes parvulus*	65
Diopatra neapolitanea	10	*Parapenaeopsis atlantica*	30
Glycera convoluta	7	*Polyonyx* sp.	51
Terebellid sp.	4	*Callianassa balssi*	11
Lumbrinereis impatiens	4	*Alpheus pontederiae*	2
Goniada multidentata	1	*Porcellana longicornis*	2
		Lyosquilla septemspinosa	2
MOLLUSCA		*Upogebia furcata*	1
Tellina nymphalis	8	*Paguristes mauretanicus*	1
Macoma sp.	5	*Diogenes pugilator*	1
BRACHIOPODA		ECHINODERMATA	
Lingula parva	2	Holothurian sp.	1
		Ophiuroidea spp.	54
GEPHYREA			
Ochetostoma mercator	14		

MYLIOBATIDAE

5. *Pteromylaea bovina* (Geoffroy St Hilaire 1809) Cownose Ray. A mixed diet of benthic invertebrates and fish is indicated for this species by the seven stomach contents available for examination.

ARIIDAE

6. *Arius latiscutatus* Gunther 1861 (Catfish). This species is very catholic in its diet, and the standard trawling results (472 stomach analyses) show fairly high percentage occurrences of penaeid and other prawns, crabs, polychaetes and fish; the food thus comprises organisms from the benthic infauna, the epifauna and actively swimming forms (Table 1).

In the area which was sampled *Arius latiscutatus* appears in a marked seasonal cycle and is very much more abundant for a short period from August-October than at any other time, so it is not possible to make a valid month by month analysis of the results. The organisms from the bulked stomach contents comprise an assortment of polychaetes and other benthic organisms listed in Table 3. It is noteworthy that relatively few fish were found in the bulked stomach contents compared with the standard trawl results where 94 of 472 individuals contained fish or fish scales, variously recorded as those of *Galeoides*, of *Sciaena* and of *Ethmalosa*. Monod (1927) records fish scales, crustacea and other benthic organisms in the diet of the related *Arius heudeloti* from the French Cameroons.

Table 3. *Food organisms identified in the bulked stomach contents of* Arius latiscutatus *with numbers of occurrences*

POLYCHAETES		CRUSTACEA	
Clymene monilis	18	*Panopeus africanus*	10
Pectinaria sourei	1	*Menippe nodifrons*	1
Goniada multidentata	1	*Heteropanope caparti*	1
Nereid sp.	1	Porcellanid sp.	2
		Callianassa balssi	4
MOLLUSCA		*Squilla africana*	1
Surcula coerulea	1		
Tellina sp.	5		
PISCES			
Unidentified fish	1		

LUTJANIDAE

7. *Lutjanus modestus* Bleeker 1863 (Grouper). The only two stomachs examined of this species both contained remains of Brachyura. Monod (1927) remarks of *L. eutactis* that it is 'carnassier' and a specimen examined by him contained a rat and the remains of a crab.

CARANGIDAE

8. *Scyris alexandrinus* (Geoffroy St Hilaire 1809) Pomp. The ten stomachs of this species examined indicated a diet based on crustaceans and small fish (Table 1).

POMADASYDAE

9. *Pomadasys jubelini* Cuvier 1830 (Crokus). A high proportion of the stomachs of this species which were examined (4176 analyses) contained polychaetes, and these, together with other organisms of the benthic infauna, appear to comprise almost the complete diet of the species in this area. Less than 5% of the stomachs contained actively swimming crustaceans, and only 2% contained fish.

The monthly analysis of the standard trawl results shows a fairly steady rate of feeding, the percentage of empty stomachs varying between 40% and 67%, with no detectable seasonal fluctuation (Fig. 1). Polychaetes are the basis of the diet and they are present in a high proportion of stomachs in almost every month of the three-year period; depressions which occur in this percentage can, in most cases, be traced to a sudden and unusual peak in the occurrence of some other food, usually *Lingula parva* or *Rotula orbicularis*. The identification of the food organisms in the bulked stomach contents confirmed the paramount importance of polychaetes in the diet. *Pectinaria sourei* was predominant among those identified, and sometimes occurred in masses filling the whole stomach. The food organisms and their frequency are shown in Table 4. The majority of these organisms are typical of the benthos of soft sandy muds in the Sierra Leone estuary, and almost all—with the exception of a very few such as *Callinectes latimanus*—are burrowing forms. Cadenat (1954) mentions small fish, crustacea, crabs, etc., as occurring in the diet of this species, and apparently the specimens that he examined (he does not state how many) had not restricted themselves so fully to the infauna as those examined in the present work.

Table 4. *The food organisms identified in the stomach contents of* Pomadasys jubelini, *with their frequency of occurrence*

NEMERTEA		CRUSTACEA	
Nemertean sp.	2	Cumacea spp.*	*c.* 5000
		Squilla africana	16
POLYCHAETA		*Polyonyx* sp.	7
Pectinaria sourei	6 241	Mysid sp.	6
Clymene monilis	44	Amphipoda spp.	5
Lumbrinereis impatiens	9	*Callinectes latimanus*	3
Glycera convoluta	9	*Lyosquilla septemspinosa*	2
Nereis succinea	4	*Panopeus africanus*	1
Terebellid sp.	3	*Porcellana longicornis*	1
Diopatra neapolitanea	3	Ostracoda sp.	1
Sternaspis scutata	2	Cirripedia sp.	1
Goniada multidentata	1		
		ECHINODERMATA	
GEPHYREA		Holothurian sp.	35
Ochetostoma mercator	3	*Amphioplus congensis*	28
Sipunculus titubans	3	*Amphipholis nudipora*	5
		Acrocnida semisquamata	4
MOLLUSCA			
Aloidis dautzenbergi	8	*Amphipholis cincta*	3
Tellina sp.	1	*Rhopalodina lageniformis*	1
BRACHIOPODA			
Lingula parva	108		

* Cumacea are probably the same species as those determined by Dr N. S. Jones from stomachs of *Galeoides*.

10. *Diagramma macrolepis* Boulenger 1890 (Hognose). The food of this species is based almost entirely upon crustaceans, and particularly upon Brachyura, which were present in 60% of the stomachs examined. Cadenat (1954) find a similar diet for this species and records Brachyura, Anomura and other crustaceans.

Table 5. *The food organisms from the stomachs of* Diagramma macrolepis

BRACHYURA		ANOMURA		MISCELLANEOUS	
Panopeus africanus	24	*Porcellana longicornis*	3	Amphipoda spp.	58
Heteropanope caparti	3			Mysids	7
Megalopa larvae	2			Carideans	3
Callinectes latimanus	1			Fish larvae	3
Brachyuran fragments	13				

The numbers taken (327) are not high enough to permit of monthly analysis, but it appears that the feeding intensity does not drop appreciably in any part of the year, nor does the predominance of crabs in the diet change. Table 1 shows the percentage occurrence of each type of food. The food organisms found in the bulked stomach contents of this species (Table 5) agree well with the findings of the standard trawling programme. With the exception of three fish larvae, all were crustaceans, of which a high percentage were brachyurans. The most commonly occurring crab (*Panopeus africanus*) is a species characteristic of the lateritic gravel deposits of the Sierra Leone estuary, and is frequently found below stones on the intertidal banks.

11. *Brachydeuterus auritus* (Valenciennes). Caiman. The sixteen stomachs which were available of this species give little information as to the diet, for the majority were empty or contained unrecognizable detritus.

SCIAENIDAE*

12. *Pseudotolithus elongatus* (Bowditch 1825) (=*nigrita* Cuv., 1830). Gwangwa. This species is typical of those that feed on mobile organisms occurring on, or near, the bottom; a fairly consistent number of stomachs was found to contain fish—about 25% of those that contained food at all, and this percentage varied little from month to month. The food organisms which occur in the highest percentage of food-bearing stomachs, however, are mysids (37%), and penaeid and other prawns (23%). In a much smaller percentage of stomachs there were remains of benthic infaunal organisms (Polychaeta, *Lingula parva*), while a few contained unrecognizable detritus. The feeding intensity varies considerably from month to month but, as Fig. 2 shows, no recognizable seasonal cycle in this variation can be seen in the results. The same is true of the percentage occurrence for the various types of food, where the variation is irregular and shows no correlation with the seasons. It is interesting that the few occurrences of *Lingula parva* were recorded in the same months in mid-1953 in which a *Lingula* peak was found in the food of several other species of fish.

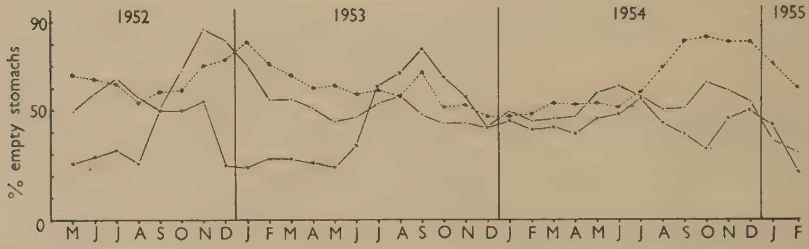

Fig. 2. The percentage of empty stomachs for three species of fish whose diet is derived from the benthic epifauna and from fish. Data from the standard trawling programme; three-period running means. ●-●-● *Pseudotolithus senegalla*; ·—·—· *P. elongatus*; X-X-X *Galeoides decadactylus*.

The results of the examination of the bulked stomach contents of this species corresponded very well with those of the standard trawl in showing the importance of small crustacea, and the virtual absence of sedentary benthic invertebrates from the diet. In each sample, except one, the number of mysids was overwhelmingly greater than that of any other food organism; in the exceptional case, the low number of mysids was balanced by a mass of cumaceans, and rather more penaeid prawns than usually occurred. Table 6 shows the identifications of the food organisms, with the number of individuals found. No difference in diet due to the size of the fish could be found when the results were analysed on a size-class basis; three classes were recognized, each of 10 cm, 10-20, 21-30, >30. The only difference that could be detected was that a higher percentage of stomachs in the 21-30 cm class contained more than one type of food than in the smaller fish, indicating perhaps, a more varied diet.

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* The nomenclature of Sciaenidae is on the authority of Dr E. Trewavas.

Table 6. Pseudotolithus elongatus: *food organisms from the bulked stomach contents*

CRUSTACEA		MOLLUSCA	
Mysidacea	1660	? *Sepiola* sp.	1
Cumacea*	90		
Parapenaeopsis atlantica	10	PISCES	
Amphipoda spp.	3	Fish larvae	2
Callinectes sp.	1	Fish remains	3
Porcellanid sp.	1		
Erychthus larva	1		
Squilla africana	1		

* Probably identical with those determined by Dr N. S. Jones from stomachs of *Galeoides*.

13. *Pseudotolithus senegalla* (Cuvier 1830) (=*brachygnathus* Bleeker 1863). Whiting. Fish form the most important constituent of the diet and occur in 75% of the food-bearing stomachs examined during the standard trawl; smaller percentages of penaeid prawns and stomatopods occurred, as is shown in Table 1. Very few specimens were available for determination of the food organisms in bulked stomach contents, and these contained only crustacea—*Parapenaeopsis atlantica* and *Squilla africana*. Cadenat (1954) found only fish remains in stomach contents of this species.

Fig. 2 shows the variation in feeding intensity over the three-year period for this species; no regular seasonal variation can be recognized.

14. *Pseudotolithus senegalensis* Valenciennes 1833. (Ladyfish). Fish are less important to this, than to the last, species, and a correspondingly higher percentage of crustaceans occurs (Table 1). I have seen no records in the literature relating to the food of this species.

15. *Pinnacorvina epipercus* Bleeker 1863. (Black trout). Sixty-seven individuals of this species was examined during the standard trawling programme, and these showed a percentage occurrence of 83% for Brachyura. Table 1 shows the percentage occurrences for all types of food.

MONODACTYLIDAE

16. *Monodactylus sebae* Cuvier 1831 (Anglefish). The stomach contents of this species show a remarkable combination of a high percentage of polychaetes, with a less high, but still important, percentage occurrence of fish. The figures are given in Table 1, and it is evident that more information on the diet is required.

EPHIPPIDAE

17. *Drepane punctata* L. 1758. (Sheepshead). The standard trawl results show that polychaetes form the basic food of this species, occurring in 84% of the food-

bearing stomachs; there were no other dominant groups in the stomach contents. *Lingula parva* occurred in a total of no more than 4% of the stomachs containing food, except for one period (January-June 1953) when it became an important constituent in the diet, and reached a peak occurrence of more than 40%. Each *Lingula* peak corresponded to a depression in the percentage occurrence of polychaetes. Crustacea occurred in less than 5% and apparently form only a minor constituent of the diet; monthly analysis confirms this, and shows few months in which their occurrence is more than 10%. The highest recorded was 24·5% in November 1954, for penaeid prawns, but this was an isolated peak. Fig. 1 gives the results of the month by month analysis of the feeding intensity.

Table 7. Drepane punctata: *food organisms from the bulked stomach contents*

POLYCHAETES		CRUSTACEA	
Clymene monilis	149	Amphipoda spp.	102
Pectinaria sourei	84	*Parapenaeopsis atlantica*	32
Glycera convulata	43	*Squilla africana*	11
Diopatra neapolitanea	12	Mysidacea	6
Nereis succinea	8	*Lyosquilla septemspinosa*	3
Lepidonotus hupferi	6	*Apseudes* sp.	2
Phyllamphicteis collaribranchus	3	*Callianassa balssi*	2
Sthenelais limicola	3		
Goniada multidentata	1	MOLLUSCA	
Sternaspis scutata	1	*Tellina* sp.	5
Magelona rosea	1	*Donax oweni*	3
Lumbrinereis impatiens	1	*Glycimeris* sp.	2
		Mactra sp.	1
BRACHIOPODA			
Lingula parva	157	COELENTERATA	
		Pennatulid sp. (?*Virgularia*)	28
PROTOCHORDATA			
Branchiostoma sp. n.	81	ECHINODERMATA	
		Ophiuroidea spp.	5
		Holothurian sp.	1

Polychaetes formed the mass of the species identified in the bulked stomach contents. A total of 311 individuals was found, in which three species predominated. Details are given in Table 7. A total of eighty-one specimens of *Branchiostoma* sp. were found, but all of these except two were taken from stomachs collected on two trips in June 1955. Similarly, all the twenty-eight specimens of pennatulids were taken from fish on a single day in August 1955.

The material of *Drepane punctata* was divided into two according to the size-classes of the fish (below and above 20 cm long), but only insignificant differences in the diet could be found when the results of the standard trawl were analysed on this basis. It is interesting to note that the percentage of empty stomachs was higher in the small fish, 25% against 12%.

18. *Chaetodipterus lippei* Steindachner 1895. (Spadefish). The diet is restricted almost entirely to the benthic infauna and to the algal and hydroid growths upon hard surfaces. Virtually no crustacea or other mobile forms are eaten, as Table 1 shows.

From July-September, during the rainy season, there is a marked drop in the number of hydroids which attach themselves to settlement plates exposed in the Sierra Leone River; no figures are available, but Mr V. Bainbridge (personal communication) has observed a heavy growth on plates exposed during the dry season, and virtually none during the rains—this at Kissy, which is farther towards the mouth of the estuary than the trawling course, and where the influence of fresh water is not so marked. The monthly analysis of the percentage occurrence of empty stomachs shows very good correlation between the feeding intensity and the rains (Fig. 3); during the latter there is a marked drop in the number of stomachs with food, reaching a minimum at the end of the rainy period in each year. This is most probably accounted for by a lack of hydroid growths in the estuary at this season. Every sample of the bulked stomach contents which was examined was found to contain, besides other food, a mass of hydroids and remains of algae which did not, of course, lend themselves to counting. The organisms identified in the stomachs are shown in Table 8. Cadenat (1954) found small crustacea, algae, hydroids and echinoderms including ophiuroids; a diet that corresponds very well to that outlined above.

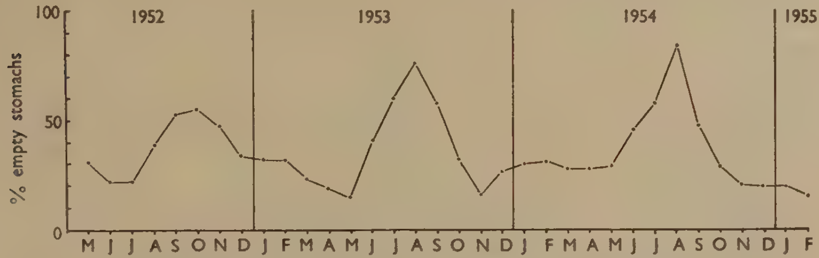

Fig. 3. The percentage of empty stomachs in the specimens of *Chaetodipterus lippei* examined during the standard trawling programme; three-period running mean.

Table 8. Chaetodipterus lippei: *the organisms identified in bulked stomach contents*

POLYCHAETA		ECHINODERMATA	
Diopatra neapolitanea	1	*Acronida semisquamata*	8
Fragmentary polychaetes	2	Ophiuroid sp.	6
		Amphipholis nudipora	1
CRUSTACEA		COELENTERATA	
Penaeid sp.	1	Hydroid skeletons	a mass
Mysidacea sp.	1		

LIOGNATHIDAE

19. *Gerres melanopterus* Bleeker 1863 (Butterfish). The ten fish which were examined indicated a diet based on the benthic infauna.

POLYNEMIDAE

20. *Polydactylus quadrifilis* Cuvier 1829. (Spanish). The standard trawl results show that fish (*Galeoides*, *Mugil*, 'eels') and large penaeid prawns are the most important items in the diet of this species, and this was confirmed by the analyses of the bulked stomach contents, in which were identified *Squilla africana*,

Parapenaeopsis atlantica and smaller shrimps, probably carideans. This species reaches a great size, and specimens weighing 25 kg are not unusual; a large individual was found dead in the estuary which proved to have eaten a full-sized Moray eel of a new species to be described by Cadenat. Fish almost certainly become a more important constituent of the diet of *Polydactylus* as it becomes larger. Devanesen & Chidambaram (1953) report a diet of crustacea and fish, including eels, for the related *Polynemus* (=*Polydactylus*) *indicus*.

21. *Galeoides decadactylus* Bloch 1795 (Shine-nose). The diet of this species is derived, in part, from the infauna of the benthos as shown by the percentage occurrence of polychaetes, and in part from the epifauna and the mobile crustacea. No seasonal variation in the feeding intensity (Fig. 2) nor in the proportions of the constituents of the diet, can be detected from the results of the standard trawling programme. Table 1 shows the percentage occurrences for each category of food.

Table 9. *Food organisms in the bulked stomach contents of* Galeoides decadactylus

BRACHIOPODA	
Lingula parva	1
POLYCHAETA	
Sthenelais sp.	9
Clymene monilis	1
Diopatra neapolitanea	1
Unidentified fragments	39
ECHINODERMATA	
Acrocnida semisquamata	6
Rotula orbicularis	4
Amphioplus congensis	2
Amphipholis cincta	2
CRUSTACEA	
Cumacea*	*c.* 25 000
Amphipoda	324
Penaeidae	29
Parapenaeopsis atlantica	15
Callinectes latimanus	17
Squilla africana	11
Penaeus duorarum	4
Panopeus africanus	4
BRACHIOPODA	
Lingula parva	1
PISCES	
Cynoglossus sp. juv.	1

* Determined by Dr N. S. Jones as *Upselaspis caparti*, *Cumopsis* sp. n.

The results of the laboratory examination of the bulked stomach contents throw more emphasis on crustacea as the most important constituent of the diet, and in numbers of individuals these far exceed the other food organisms; this is shown in Table 9. Of these species, the penaeid prawns, the fish and the *Callinectes* are all actively swimming animals, while the remainder are benthic; the very large numbers of small crustacea which occur are characteristic of the stomach contents of this species. At times the stomachs have been found to contain a compact mass of fine vegetable fibres and cumaceans.

Monod (1927) found this to be an active predator, and identified *Callinectes*, *Ethmalosa* and *Syngnathus* in its food, while Cadenat (1954) found that small crustacea, echinoderms, etc., were included in the diet, the latter list agreeing more with that presented here.

PSETTODIDAE

22. *Psettodes belcheri* Bennet 1831 (Dogsole, Flounder). Only eleven specimens were available for examination, and of these a high proportion were empty; the

remainder all contained (Table 1) either fish or cephalopods, and an active ichthyophagous diet is indicated.

SOLEIDAE

23. *Synaptura punctatissima* Peters 1876 (Sole). The only food found in the twenty-three stomachs examined consisted of polychaetes and fish. The numbers are too low for any conclusions to be drawn as to the nature of the diet.

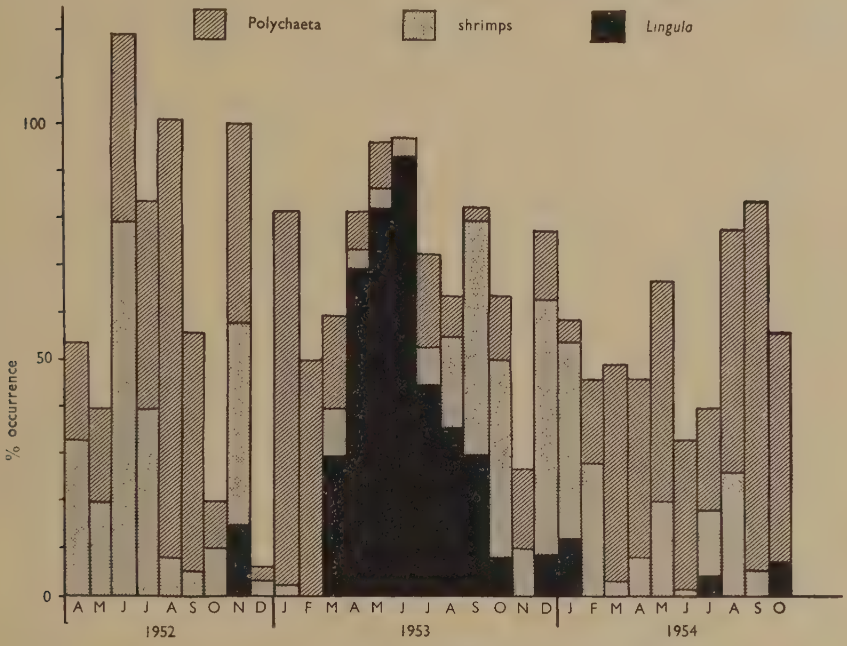

Fig. 4. Percentage occurrence of three elements in the diet of *Cynoglossus senegalensis*.

CYNOGLOSSIDAE

24. *Cynoglossus senegalensis* (Kaup 1858) (Kissy Sole). It is likely that with this species were confused some specimens of *C. goreensis* Steindachner 1892, which is known to occur in the Sierra Leone estuary. This species feeds almost exclusively upon the benthic infauna, and the vagile fauna of the estuarine bed is of very little importance to it. The rate of feeding is fairly constant, with no major fluctuations, and with no apparent regularity in the small-scale fluctuations. Fig. 4 shows the results of an analysis of the occurrence of the three main food components. Polychaetes and small crustacea form the bulk of the diet, the former perhaps being the most important and occurring in 31% of the food-bearing stomachs. Almost all the *Lingula parva* which were recorded occurred in a short period in mid-1953 when the occurrence was as high as 93%. The variations in the percentage occurrence of polychaetes, which may be regarded as the basic

food, are reflected in the occurrence of the other foods. When fewer polychaetes are eaten, shrimps occur in a higher proportion of stomachs. During the period March-September 1953, when the occurrence of *Lingula parva* became abnormally great, there was a corresponding decrease in the percentage occurrence of all other types of food; a similar effect can be seen in October 1952, when an unusually high percentage of Brachyura (72·7%) occurred.

Table 10. *Food organisms identified in the bulked stomach contents of* Cynoglossus senegalensis

POLYCHAETA		CRUSTACEA	
Pectinaria sourei	4	*Squilla africana*	10
Glycera convoluta	4	*Panopeus africanus*	2
Terebellid sp.	3	*Menippe nodifrons*	1
Sthenelais sp.	2	Porcellanid sp.	1
Goniada multidentata	1		
Eunice sp.	1	ECHINODERMATA	
Polychaete fragments	19	*Rotula orbicularis*	1
GEPHYREA		MOLLUSCA	
Ochetostoma mercator	1	*Iphigenia truncata*	2
		Tellina sp.	1
BRACHIOPODA			
Linglua parva	8		

The food organisms identified from the bulked stomach contents included nine species of polychaetes, and six of crustacea, and these form the most important constituent of the diet; these and the other organisms identified are listed in Table 10. The soles examined on the standard trawling programme have been arranged in four size-classes, and some differences in diet during growth are detectable. These figures are shown in Table 11. There appears to be an increase in the percentage occurrence of some components of the diet (Brachyura, Polychaeta) during growth, and a corresponding decrease in the percentage of empty stomachs. The implications of the latter are discussed elsewhere.

Table 11. Cynoglossus senegalensis: *distribution of percentage occurrences of various components of the diet according to size-classes*

	Size-Group (cm)			
	<20	21-30	31-40	>41
% empty	67·7	59·4	59·5	44·8
% occurence of:				
Polychaeta	25·3	22·1	64·2	57·3
Penaeids	11·4	4·6	6·3	12·2
Brachyura	17·3	11·8	21·7	25·8
Stomatopoda	–	2·5	9·4	10·1
Lingula	11·4	39·6	23·8	9·7
Rotula	8·5	–	–	–
Detritus	14·3	31·0	9·8	8·9

TETRAODONTIDAE

25. *Lagocephalus laevigatus* L. 1758 (Smooth Puffer). Only two specimens of this species have been examined, and both were found to contain molluscs. Cadenat (1954) remarks on the voracity of this fish, and the variety of its diet, which he finds to include crustacea, fish and vegetable debris.

26. *Hemiconiatus guttifer* Bennett 1831. (Common Puffer). The fifty-nine specimens of this species which were examined are probably an adequate sample from which to estimate the diet, and this appears to be as catholic as Cadenat found for the previous species. Table 1 shows that a high proportion of stomachs in which food was recognizable contained the shells of oysters; less important are cirripedes, *Rotula orbicularis* and various molluscs.

DISCUSSION

In the Sierra Leone estuary, as in other tropical waters, the seasonal variation in the water temperature, though regular, has no great range. Mr J. C. D. Watts (unpublished) finds a temperature range of less than 5° C between the coldest bottom water and the warmest surface water in the estuary over a two-year period, and a seasonal variation of 3-4° C at a single station in mid-estuary. The water temperature is therefore unlikely at any period of the year to have an inhibiting effect on the feeding rate, such as occurs in northern areas.

In the area of the standard trawl there is a considerable drop in salinity during the rainy season, reaching a maximum depression in August and September. This, together with the increase in the speed of the tidal streams, forms the main seasonal environmental change likely to affect the fish. Figs. 1 and 2 show how little, in fact, this change does affect the feeding rate of some of the fish; the variation in the percentage of empty stomachs is shown for six species of fish and is very small compared with that found by Todd (1915) for North Sea plaice (*Pleuronectes platessa*), where the winter figure was about 90% empty, the summer 1%-2% empty. Tham Ah Kow (1950) found that the fish, both pelagic and demersal, of the Singapore Straits continued to feed throughout the year, the feeding intensity being variable within relatively narrow limits; it is unfortunately not possible to make direct comparisons with his results, for he gives no figures for the number of stomachs found to be empty in relation to the total number examined.

Fig. 1 shows a peak in the percentage of empty stomachs in *Drepane punctata* and in *Pomadasys jubelini* during the rainy season of 1953 (peaks July-August and June-August) but these were not repeated in the other two years nor does this peak occur in the other species with a similar diet, *Trygon margarita*, which is also included in the figure. In Fig. 2 are shown the data on the feeding intensity of three species which feed on the epifauna and fish, and it will be seen that here too there is little evidence of any seasonal variation unless it is a tendency for the peaks in the graph (*i.e.* a low feeding intensity) to occur during the dry season from

October to May. Fig. 3 shows, however, that in *Chaetodipterus lippei* there is a clear seasonal variation in the feeding rate, the peaks in the percentage of empty stomachs all occurring at the ends of the rainy seasons. This species has a much more specialized diet than those already considered, and its staple food is known to be much reduced in abundance during the rainy season (p. 378). It is reasonable to suppose that the relative specialization of the diet prevents this species from turning to another food when the staple becomes scarce, as perhaps happens in the case of species with a more varied diet. For instance, Fig. 4 shows the way in which this may occur in *Cynoglossus senegalensis*, though the variation in diet appears to be irregular rather than cyclical. Probably a more detailed study of a single species, in which all the food organisms are precisely determined over a similar period, would reveal a shift from one species to another from season to season. No evidence has been found to demonstrate a regular shift, even from one phylum of food organisms to another, in the present work.

There appears to be some evidence in Table 1 that the species in which fish form an important constituent of the diet tend to have a high proportion of empty stomachs. If the species in which more than fifty specimens were caught are analysed this is clearly seen, two species which eat fish showing 51% of empty stomachs, six species which eat epifauna and fish 37·1%, and eight species feeding on the infauna 33% of empty stomachs. Inspection of Table 1 will reveal many discrepancies to this, but the generalization appears to be valid and corresponds with what is known of the relative food values of the various food organisms. Jones (1954) quotes Hertling (1938) as showing that the calorific value of fish is weight for weight considerably higher than that of, for instance, crustaceans. It may be that the daily intake of ichthyophagous species can be lower than those whose diet is based on benthic invertebrates. Also, fish being relatively large organisms, their intake as food will tend to be discontinuous, compared with the more or less steady cropping of invertebrate food.

A tendency for the smaller fish to have a higher proportion of empty stomachs (*e.g. Cynoglossus senegalensis*) than those included in the larger size groups is inexplicable with the present evidence, and is quite contrary to what Jones (1954) finds in *Gadus merlangus* and attributes to differential disgorging in the cod-end of the trawl. The explanation for a higher percentage of empty stomachs both in small fish and in fish-eating fish may in fact lie in differential disgorging. In a species with a mixed diet, in which few fish occur, the smaller specimens may become relatively more crushed in the trawl, and so more frequently disgorge; also those species which are ichthyophagous may tend to disgorge their single, large, food masses more completely than if their stomachs contained many small organisms, of which some could remain behind and so be recorded. Jones's large *Gadus* contained relatively more fish than the smaller specimens.

The selection of the benthic organisms as food from those available will be discussed in a later publication, when the survey of the benthic communities is complete, but it is clear from the results in the present work that the organisms that form the basis of the food of those fish which feed on the bottom fauna are common, and often dominant, species in the benthic communities, especially those of the muddy sand deposits.

It is remarkable that on a number of occasions a species of fish has been found to turn from its usual food organisms and take, for a limited period, large quantities of a relatively unusual food. The clearest example of this is in the case of the small brachiopod *Lingula parva*. Table 12 shows its percentage occurrences in the stomachs of six species of demersal fish over the whole three-year period, and it is at once apparent that the vast majority of *Lingula* that were eaten by these fish were taken during a relatively short period covering the latter part of the dry season and the first half of the rainy season of 1953. Outside this single period the occurrence of this species as food is very sporadic, but during it some species almost abandoned their normal diet in favour of *Lingula* (*e.g. Cynoglossus*, Fig. 4). This could be due to three reasons: a sudden lack of the usual diet, a sudden disaster to the *Lingula* population due to currents scouring the mud-banks in which they live, or an unusually abundant settlement of larvae in the estuary resulting in an unusually dense brachiopod population. There is no evidence for the first possibility; Mr A. G. Taylor has pointed out to me that the period concerned begins during the time of minimum scouring in the estuary, and it seems most likely that the correct answer is the last possibility. Mr V. Bainbridge finds that larvae of *Lingula* are present in the plankton at the mouth of the estuary for most of the year, but very rarely at a plankton station in mid-estuary; this is a marine euryhaline species which is able to invade the estuary during the dry season more successfully in some years than in others. The data show similar but less spectacular peaks in the occurrence of other food organisms in the stomach contents for

Table 12. *The percentage occurrence of* Lingula parva *in the stomach contents of six species of demersal fish*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1952 and 1955	1955			1952								
Pomadasys jubelini	4·4	–	2·8	–	1·1	–	–	–	–	–	2·1	–
Drepane punctata	–	9·0	–	1·3	3·9	–	–	–	–	–	6·6	–
Chaetodipterus lippei	–	–	–	–	16·6	–	–	–	–	–	–	–
Galeoides decadactylus	–	–	–	–	10·5	–	–	–	–	–	–	–
Cynoglossus senegalensis	14·2	–	4·5	–	–	–	–	–	–	–	14·0	–
1953												
Pomadasys jubelini	–	44·4	75·8	46·0	50·0	15·6	28·5	6·0	–	–	2·1	–
Drepane punctata	–	45·4	–	35·0	28·0	32·0	–	6·2	7·6	6·1	–	3·2
Pseudotolithus elongatus	–	3·5	4·4	–	–	–	1·1	–	–	–	–	–
Galeoides decadactylus	–	44·7	–	–	12·0	32·2	–	56·0	–	–	–	–
Cynoglossus senegalensis	–	–	30·0	68·9	80·9	93·7	44·4	35·4	30·2	6·4	–	8·8
1954												
Pomadasys jubelini	–	1·8	–	–	–	–	–	–	22·2	–	–	–
Drepane punctata	–	–	0·4	–	–	–	–	–	–	–	–	–
Galeoides decadactylus	–	–	–	2·0	1·5	3·3	–	–	–	–	–	–
Cynoglossus senegalensis	12·0	8·1	–	–	–	–	3·5	–	–	7·1	–	–

short periods only. There was, for instance, a peak in the occurrence of the small sand-dollar *Rotula orbicularis* in the stomachs of *Pomadasys jubelini* between December 1953 and May 1954, with a maximum percentage occurrence of 55·7 in February 1954. There is no corresponding peak in either of the other two years of the standard trawl.

The situation shown in Fig. 4 for *Cynoglossus* is typical of that found in most of the species of benthos-feeding fish for which there was sufficient information, and it is thought that the general complexity of the estuarine environment is causing the constant shift of the percentages of the various food organisms in the diet, and this, together with the lack of a depressant winter period, probably results in the observed haphazard variation in the diet combined with the continual, though small-scale, variations in the feeding intensity.

ACKNOWLEDGMENTS

I am very grateful to the Director of this Institute, Mr A. G. Taylor, for permission to use the data on stomach contents collected during his standard trawling programme; and to my colleagues who assisted in collecting it, often under very uncomfortable conditions. For the identity of food organisms I have to thank many systematists, to whom I have submitted material taken during the benthos survey, and whom I shall acknowledge severally in a publication on that subject. Mr J. C. D. Watts of this Institute, has provided all the hydrological data.

SUMMARY

1. The demersal fish of the Sierra Leone River can be divided into three categories on the basis of their diet: those which are almost exclusively ichthyophagous, those which feed on the more active members of the invertebrate epifauna together with some fish, and those whose diet is based on the invertebrate infauna and the sedentary epifauna.

2. The percentage composition of the diet of individual species is constantly and irregularly changing, and no seasonal correlation has at present been observed in most species.

3. There are several instances of fish turning from their normal food to a food organism which normally occurs in their stomachs only rarely, and for a short and isolated period eating it almost to the exclusion of other foods.

4. The fish feed throughout the year, feeding intensity varies within relatively narrow limits, and in most species this variation appears to have no seasonal basis. One species is exceptional, in that the results show a marked cyclical depression of the feeding intensity during the wet season, which could be correlated with a corresponding scarcity of its staple food.

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THE BIOLOGY OF *CENTRONOTUS GUNNELLUS* (L.) (TELEOSTEI)

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(With Plate 7 and 6 Figures in the Text)

Centronotus gunnellus (L.) is a widely distributed northern fish, being found on both sides of the Atlantic, reaching west Greenland, Spitzbergen and other regions of the Arctic Ocean in the north (Duncker & Mohr 1928, Saemundsson 1949). On the east American coasts, owing to colder sea temperatures, it penetrates as far south as Massachusetts (Breder 1948), but on the European coasts it reaches its southern limit in the English Channel. It is of common occurrence on almost all the coasts of the British Isles (Day, 1880-84).

Table 1. *Numbers of fish in each centimetre length-group caught in each month*

	1954											1955				
Length (cm.)	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
6·0	–	–	–	–	–	4	–	–	1	1	No sample	2	1	2	1	–
7·0	–	–	1	–	–	–	–	3	1	–		5	4	3	5	2
8·0	1	3	2	–	–	–	–	1	–	–		2	1	2	2	4
9·0	4	1	4	–	1	–	–	–	1	–		1	1	–	1	1
10·0	1	4	1	1	1	–	1	–	–	–		–	–	1	1	–
11·0	1	–	7	2	–	–	1	–	–	1		1	1	3	1	5
12·0	1	1	–	5	–	–	1	–	2	2		2	1	8	5	8
13·0	–	1	2	1	–	2	–	–	2	3		1	3	10	5	7
14·0	–	2	3	2	1	3	3	–	–	–		1	3	6	13	4
15·0	1	–	–	2	6	1	2	–	–	1		1	1	5	6	4
16·0	2	–	2	2	1	1	3	–	–	–		–	–	2	2	1
17·0	–	–	–	–	1	2	1	1	–	–		–	–	–	–	4
18·0	–	–	–	–	–	1	–	–	–	–		–	–	1	–	–
Total	11	12	22	15	11	14	12	5	7	8		16	16	43	42	40

The nesting and incubating habits of this species are well known and have been studied by several earlier authors, including Smith (1887), Holt (1893), Ehrenbaum (1904) and Gudger (1927), who also gave the breeding season, as deduced by the occurrence of eggs on the shore. Other works on this species include descriptions of the eggs (McIntosh & Prince 1890, Ehrenbaum 1904), morphology of the larvae (Ehrenbaum 1905), and more recently brief accounts of the experiments on rearing the larvae (Qasim 1955) and the breeding cycle, which seems to be correlated with the Arctic-boreal distribution of the species (Qasim 1956*a*). There is, however, no information yet available about its growth-rate, gonad maturation or food.

Centronotus gunnellus occurs low down on the shore, mainly in the region of low water spring tides, amongst *Laminaria*. The fish were obtained by turning over stones, under which they usually lie hidden. When thus disturbed the fish become very active, making it difficult to seize them by hand. The species has been seen on the shore throughout the year except in December, when probably it moves into deeper water. Larger specimens have been caught occasionally in a shrimp trawl at depths of 30-40 ft at all times of year.

Monthly collections were made between February 1954 and May 1955 from the shores of the Menai Straits. All the fish obtained were preserved in 70% alcohol and examined as soon as possible. The examination of each fish included measuring its length to the nearest centimetre below, weighing it to the nearest 0·5 gm, determining the sex by internal examination, assessing the state of maturity of the gonads, analysing the gut contents, and extracting and mounting the otoliths.

GROWTH

The length frequency distribution of 274 specimens, caught during a period of sixteen months, is given in Table 1. The data were grouped into four quarterly seasons, each of three months, the spring quarter including all the data from March to May of both 1954 and 1955, and so on. These results are shown as histograms in Fig. 1. An examination of this figure gives little information about the age and growth. The O group can be distinguished in size only during summer and probably during autumn, but the interpretation can be taken no further. The absence of any further distinction of age-groups suggests that the size range in any age-group is large as compared to its annual increase in length. This was confirmed by otolith readings.

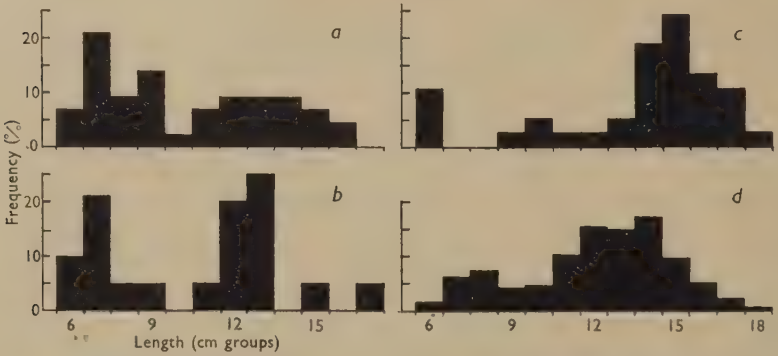


Fig. 1. Length-frequency distribution of *Centronotus gunnellus* in various quarterly seasons. *a*, Dec.-Feb.; *b*, Sept.-Nov.; *c*, June-Aug.; *d*, March-May.

The otoliths of *Centronotus gunnellus* have been figured by Scott (1906). They show definite concentric zones, on which the present study of the growth-rate has mainly been based. The technique of their extraction and preparation was essentially the same as used in *Blennius pholis* L. (Qasim 1957). Out of the total number examined, about 7% were found unreadable. When the otoliths are examined under a dissecting microscope by reflected light, alternate opaque and

Table 2. *Numbers of fish of various lengths in age-groups 0 to 5+, as determined by otolith readings*

Length-groups (cm)	Males								Females							
	Total frequency	0	1+	2+	3+	4+	5+	Unreadable	Total frequency	0	1+	2+	3+	4+	5+	Unreadable
6·0	5	4	1	–	–	–	–	–	7	4	3	–	–	–	–	–
7·0	13	5	8	–	–	–	–	–	11	6	5	–	–	–	–	–
8·0	11	3	7	–	–	–	–	1	7	1	6	–	–	–	–	–
9·0	6	–	4	2	–	–	–	–	9	1	5	3	–	–	–	–
10·0	1	–	–	–	–	–	–	1	10	–	1	7	1	–	–	1
11·0	7	–	–	4	2	–	–	1	16	–	–	10	6	–	–	–
12·0	16	–	–	6	8	2	–	–	20	–	–	6	11	2	–	1
13·0	14	–	–	3	3	6	–	2	23	–	–	3	14	5	–	1
14·0	22	–	–	–	9	8	1	4	19	–	–	1	9	5	1	3
15·0	16	–	–	–	7	5	2	2	14	–	–	–	4	7	2	1
16·0	8	–	–	–	2	4	2	–	8	–	–	–	–	6	2	–
17·0	5	–	–	–	–	3	2	–	4	–	–	–	–	2	1	1
18·0	1	–	–	–	–	–	1	–	1	–	–	–	–	–	1	–
Total	125	12	20	15	31	28	8	11	149	12	20	30	45	27	7	8
Mean length	–	7·30	8·13	11·92	13·99	14·88	16·20	–	–	7·27	8·16	11·45	13·23	14·97	16·34	–

transparent zones become visible (Pl. 7). The central area of the otolith was found to be variable in appearance. In some, it was completely opaque whilst in others it was largely opaque but contained a transparent area in the middle. The latter condition was always the predominant one. The transparent zones, as a rule, are broad and easy to distinguish from the intervening opaque zones.

The ages of the fish were estimated by counting the number of transparent zones, excluding that in the middle of the central area, on the assumption that one of these is laid down annually. Individuals with otoliths showing only the centre were called O group. It must be admitted that since age-groups, other than the O class, cannot be distinguished from the size-frequency distribution, no other conclusive evidence is given that the zones on the otoliths are annual. The assumption is therefore based on analogy with the annual character of the zones in other fish (Graham 1929).

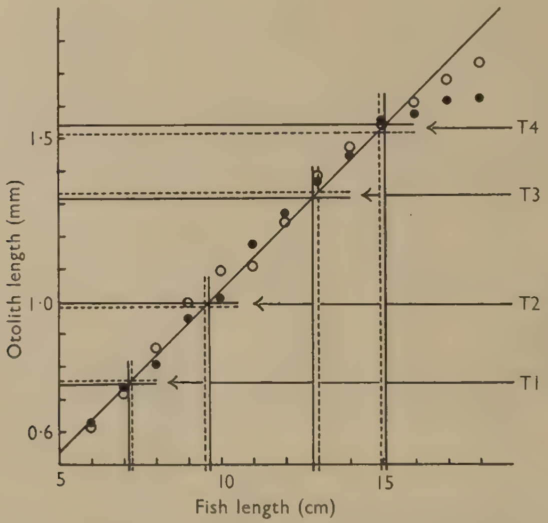
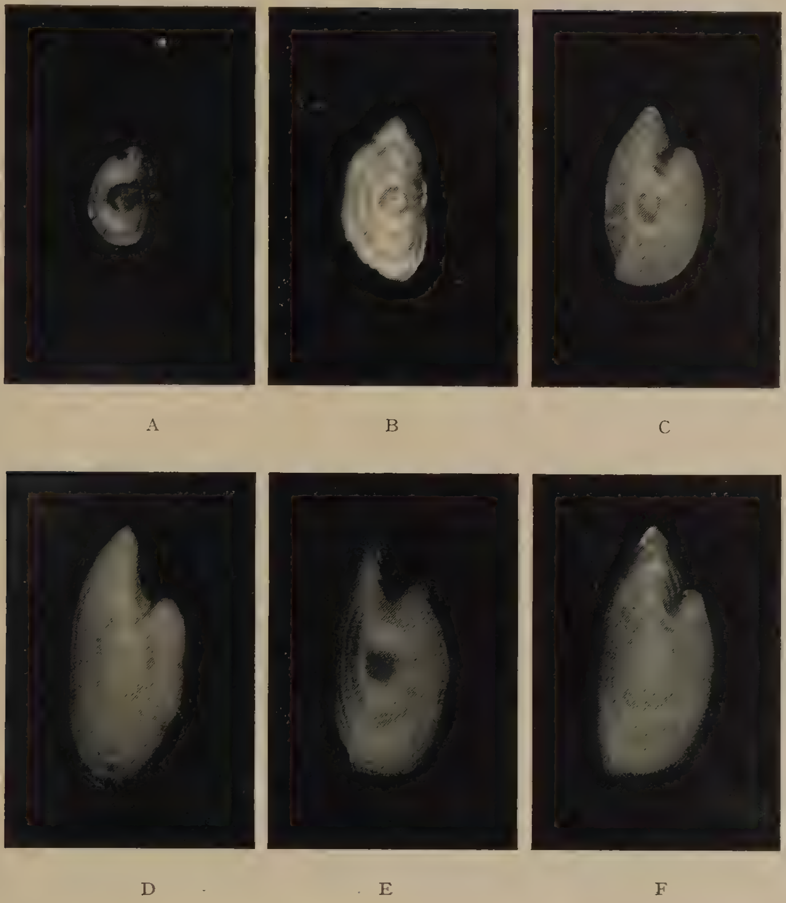


Fig. 2. The relation between the length of fish and the length of the otolith. ○, male; ●, female. The horizontal lines T_1-T_4 drawn from the vertical axis and cutting the correlation curve represent the mean lengths of the first four transparent zones on the otolith. The vertical lines joining the horizontal axis and the cut give the respective lengths of fish corresponding to various transparent zones. - - - -, male; ——, female.

The length-frequencies of both sexes corresponding to various age-groups are given in Table 2, together with the mean lengths of each age class. It can be seen from the table that for every age-group there is an overlap of several centimetres in both sexes. A fish measuring 12-13 cm in length, may belong to any age-group from 2 to 4. Apparently there is such a large size range in all the age-groups that analysis of the length-frequency distributions gives little indication of the size-frequency of the various year-classes. The mean lengths of the age-groups in Table 2, give estimates of the sizes of the fish at about the middle of each year of



Otoliths of *Centronotus gunnellus* photographed by reflected light against a black background, × 20. The number of transparent (dark) zones corresponds to the presumed age of the fish.

A, one-year-old male 7·0 cm long;
B, two-year-old female 11·7 cm long;
C, three-year-old female 12·8 cm long;
D, four-year-old male 15·5 cm long;
E, five-year-old male 15·7 cm long;
F, five-year-old female 16·0 cm long.

life. A further study to determine their sizes at the end of each year of life, *i.e.* when each of the transparent zones is laid down, was made from back calculations, as follows. The lengths of all the otoliths used for age determination were measured under a micrometer eyepiece and the mean values corresponding to each centimetre length-group were calculated. These have been plotted in Fig. 2, and given in Table 3, with their standard deviations. As can be seen from the figure, the points lie approximately in a straight line, except in the largest size range where the relative lengths of the otolith appear slightly smaller. This may be because the data referring to these were obtained from fewer measurements. At first it was thought that this condition might be due to negative heterogonic growth of the otolith, as found in *Blennius pholis* (Qasim 1957), but when these points were plotted as logarithms, the regression coefficient was found to be:

Table 3. *The relationship between the length of the fish and the length of their otoliths*

Length-groups (cm)	Number of otoliths measured	Mean otolith length (mm)	S.D.	Number of otoliths measured	Mean otolith length (mm)	S.D.
6·0	10	0·615	0·101	13	0·618	0·116
7·0	25	0·709	0·044	22	0·724	0·041
8·0	22	0·855	0·125	12	0·807	0·080
9·0	12	0·994	0·097	18	0·946	0·103
10·0	2	1·090	–	20	1·080	0·167
11·0	14	1·109	0·043	32	1·175	0·121
12·0	32	1·240	0·117	40	1·266	0·119
13·0	28	1·380	0·149	46	1·370	0·135
14·0	44	1·470	0·170	38	1·445	0·115
15·0	32	1·540	0·141	28	1·545	0·132
16·0	16	1·610	0·167	16	1·570	0·205
17·0	10	1·680	0·070	8	1·614	0·154
18·0	2	1·730	–	2	1·620	–

$$\mathrm{Log}_{10}\ L = 0{\cdot}97 \log_{10} l + 1{\cdot}96$$

or $L = 91{\cdot}2\, l^{\,0\cdot97}$

almost $L = 98\, l^{\,1\cdot0}$ (in both sexes)

where L = length of the fish and l = length of the otolith.

Therefore the growth of the otolith was considered to be proportional to the length of the fish, within the limits of the available data.

Table 4. *Mean lengths of the first four transparent zones and the back-calculated length of fish corresponding to various zones*

Transparent zone	Total no. measured	Mean length (mm)	S.D.	Back-calculated lengths (cm)
MALES				
I	30	0·756	0·067	7·20
II	21	0·980	0·102	9·50
III	20	1·330	0·120	13·00
IV	15	1·512	0·094	15·00
FEMALES				
I	30	0·747	0·058	7·10
II	23	0·992	0·106	9·60
III	20	1·315	0·082	12·85
IV	14	1·537	0·077	15·10

The lengths of the first four transparent zones in all easily readable otoliths were measured under a micrometer eyepiece and the mean values for each sex are given in Table 4. Using these values, the lengths of the fish during the formation of the first four transparent zones were back-calculated by the graphical method, as shown in Fig. 2. These lengths have also been included in Table 4.

The length estimates obtained from direct otolith readings and from back calculations have been plotted as a growth curve in Fig. 3. The values corresponding to age-group 5+ are probably not very reliable on account of the small numbers available. It is evident from the curve that both sexes grow at approximately the same rate, which seems to be fairly uniform throughout life. There is, however, considerable individual variation in the growth-rate among individuals belonging to the same year class, since the range in length in all the age-groups is large.

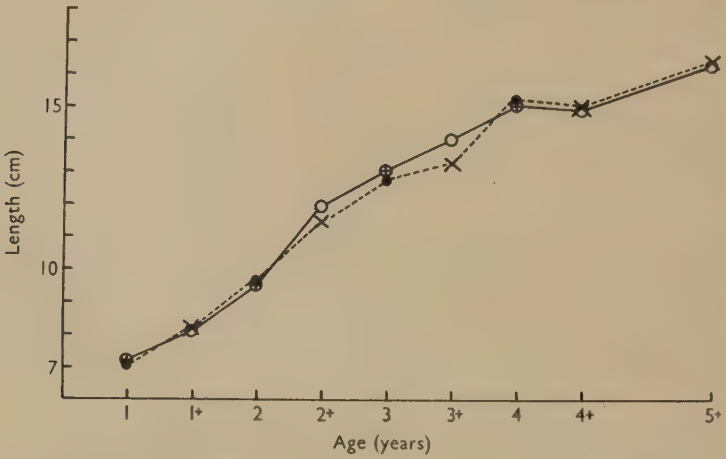


Fig. 3. Growth of *Centronotus gunnellus*; - - - -, male; ——, female. Mean lengths of the age-groups determined by otolith readings (O, male; X female) correspond to the middle of each year. The back-calculated lengths (⊕, male; ●, female) correspond to the end of each year.

BREEDING

(*a*) *The breeding cycle*

The sexual organs in *Centronotus gunnellus* consist of a single ovary in the female and a pair of testes in the male (Smith 1892-95, Jenkins 1936). The degree of maturity of the gonads in each individual examined by the naked eye was determined according to the following arbitrary scheme: (i) immature (gonads thin and ribbon like); (ii) maturing virgins or recovered spents (ovary containing eggs just visible to the naked eye, testes enlarged and yellowish in colour); (iii) ripening (ovary larger, containing conspicuous opaque eggs, testes considerably swollen and yellowish white); (iv) ripe (ovary filling the whole of the body cavity and containing large translucent eggs, testes milky white with milt extruded by slight pressure); (v) spent (ovary collapsed, containing some residual eggs, testes shrunken and yellowish brown). Young and immature individuals, the sex of which could not be ascertained by the naked eye, were examined under a microscope. All fish measuring 6-8 cm in length had to be classed as immature. From 9 cm onwards, stages of advancing maturity were recorded in both sexes, and at 10 cm both ripe and spent stages were commonly seen. It therefore appears that both sexes begin to mature when they are about two years of age and between 9-10 cm in length.

Monthly percentages of gonads at each maturity stage are shown in Fig. 4, except in December when no samples were available. The data obtained from February to May 1954 and the corresponding period in 1955 were combined together in the figure. It can be seen that the gonads in all mature fish show a regular seasonal change without much individual variation. From June to August all the fish likely to spawn during the forthcoming breeding season reach the maturing stage (ii). This is followed by the ripening stage (iii) during autumn. In December, when the fish are presumably ripe, no samples were available on the shore, but in January and February, when they reappear, the samples include both ripe and spent fish. In March all the fish examined from 10 cm and above in length were completely spent, and the same condition was seen in April and May. It can therefore be concluded that January and February are the main spawning months. The small number of ripe fish caught during January and February (five males and two females) and the rapid increase in the proportion at the spent stage clearly suggest that spawning in each individual lasts for a short time. Further evidence that spawning in each individual is short and occurs once a year only can be obtained by examination of the gonads of the guardian fish. Out of the total of nineteen females and nine males examined all but two had spent gonads. The two exceptions were males, which unlike females may therefore be sometimes capable

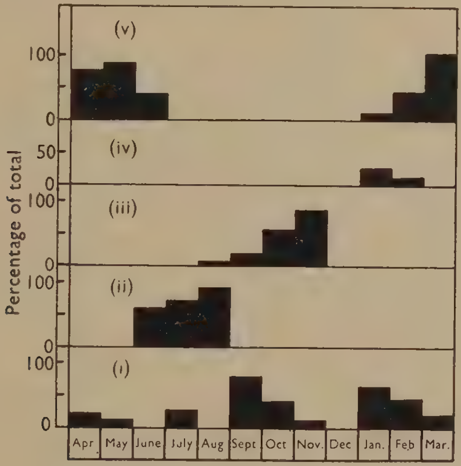


Fig. 4. Monthly percentages of gonads at each of five maturity stages (see text, p. 394).

of spawning more than once. The act of spawning in all females and most males therefore seems to take place at a definite and quite short period during winter and early spring.

Previous authors give the breeding season as February to April at Loch Creran (Smith 1887), February and March at St Andrews (McIntosh & Prince 1890, Holt 1893), probably December and January at Helgoland (Ehrenbaum 1904), late in the winter around the coasts of Iceland (Saemundsson 1949). From these accounts, it appears that spawning occurs almost at the same time throughout the geographical range. This type of breeding is characteristic of Arctic-boreal species (Qasim 1956*a*), and is in direct contrast to the habit of producing multiple broods over a much longer period later in the year shown by southern species such as the common shore fish *Blennius pholis* (Qasim 1956*b*, 1957).

(*b*) *Care of eggs by parents*

The eggs are found in abundance during January, February and March, the earliest having been recorded on 17 January. Almost all the egg masses collected in March were well advanced in development and those obtained towards the end of March hatched within a few hours after collection. In 1954 the last egg mass was found on 4 April, but in 1955, in spite of intensive and repeated efforts, only one egg mass was seen during the last week of March and none later on. No egg mass was ever found unattended. In this species, both sexes have been been reported to guard the egg masses during the incubation period (Smith 1887, Holt 1893, Ehrenbaum 1904). The sex determination of all the parents taken from each egg mass, as given in Table 5, showed that it is quite usual to find both sexes guarding the eggs earlier in the season, but when the season advances this duty seems to be mainly taken up by the females. Out of the total of twenty egg masses taken with parents, only one instance of the male alone guarding the eggs was found. Fish caught during the breeding season not guarding eggs included both sexes with males in the majority. Perhaps both parents take turns in guarding or perhaps only one more devoted parent, generally the female, sticks to its task until the end. Since males are not always spent after spawning, they may move on to pair with other previously unmated females. The females, since they are always completely spent after the spawning and cannot reproduce until the following year, are best occupied in guarding the eggs. Such female guardianship is rarely, if ever, found in more southern species such as *Blennius pholis*. In these the eggs are guarded, if at all, by the males, leaving the females free to feed, and so better able to mature successive batches of eggs (Qasim 1956*a*).

On several occasions, a guarded egg mass was picked up from its natural position on the shore and placed about 30 cm away, without disturbing the parents unduly. None of the two fish made any attempt to move towards the eggs. The egg mass was then placed closer to the parents in gradual steps. When it was only about 15 cm away, one fish of the pair made a quick serpentine movement and curled round the eggs again. The process was repeated once more with the same fish and also with its mate. When two fish were present one, probably the female, responded,

Table 5. Centronotus gunnellus: *size, sex, food and state of maturity of gonads in parents*

	Egg mass	Length of fish (cm)		Gut contents													Gonads
				Polychaeta	Isopoda	Amphipoda	Crabs	Barnacles	Copepoda	Gastropoda	Algae	*Caprella*	Pycnogonids	Insect larvae	Sand and gravel	Unrecognizable food	
1954																	
Feb.	1	16·6	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
		16·2	♂	–	–	–	–	–	–	–	–	–	+	–	–	–	spent
Mar.	2	14·8	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
		14·1	♂	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
	3	13·1	♀	+	–	–	–	–	–	–	–	–	–	–	–	–	spent
	4	10·0	♀	–	+	+	–	–	–	–	–	–	–	–	–	–	spent
Apr.	5	14·0	♀	+	+	+	–	–	–	–	–	–	–	+	+	–	spent
1955																	
Jan.	6	13·7	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
		15·5	♂	–	–	–	–	–	–	–	–	–	–	–	–	–	ripe
	7	12·7	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
		14·7	♂	–	–	–	–	–	–	–	–	–	–	–	+	–	ripe
Feb.	8	12·7	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
		13·5	♂	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
	9	14·2	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
		15·0	♂	+	+	+	–	+	–	–	–	–	–	–	–	–	spent
Mar.	10	14·1	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
		15·2	♂	–	–	–	+	–	–	–	+	–	–	–	–	–	spent
	11	15·3	♀	+	–	–	–	–	–	–	–	–	–	–	–	+	spent
		15·8	♂	+	+	+	–	–	+	+	–	–	–	–	–	+	spent
	12	13·6	♀	–	+	–	+	–	–	–	–	–	–	–	–	–	spent
	13	14·9	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
	14	12·8	♂	+	–	–	–	–	–	+	–	–	–	–	–	+	spent
	15	13·7	♀	+	–	–	–	–	–	–	–	–	–	–	–	–	spent
	16	12·5	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
	17	12·7	♀	–	–	–	–	–	–	–	+	–	–	–	+	–	spent
	18	12·3	♀	–	–	–	–	+	–	–	–	–	–	–	–	–	spent
	19	11·7	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent
	20	11·6	♀	–	–	–	–	–	–	–	–	–	–	–	–	–	spent

but when this fish was removed its mate showed the same response although it had not done so when parents were on guard. Further attempts to demonstrate their behaviour to witnesses on the shore were fruitless. Storrow (1915) made similar observations.

(*c*) *Condition factor*

Seasonal analysis of the length-weight relationship as based on the 'condition factor' has been used as an index of spawning in several other species of fish (Thompson 1942, Le Cren 1951). Throughout the present study the condition factor of each fish was calculated from the formula $K = 100\,W/L^3$. The results are given in Fig. 5. This shows that both sexes were poorest in condition during March, after the period of incubation. From April onwards, when normal feeding was resumed (see below), the condition factor began to rise, reached highest values in June, and remained high throughout autumn and early winter. The rapid fall during January and February coincides with the spawning season. During March, when most of the spent fish are engaged in parental care, feeding almost ceases. This is probably the time when remaining reserves are utilized, producing minimum values for the condition factor.

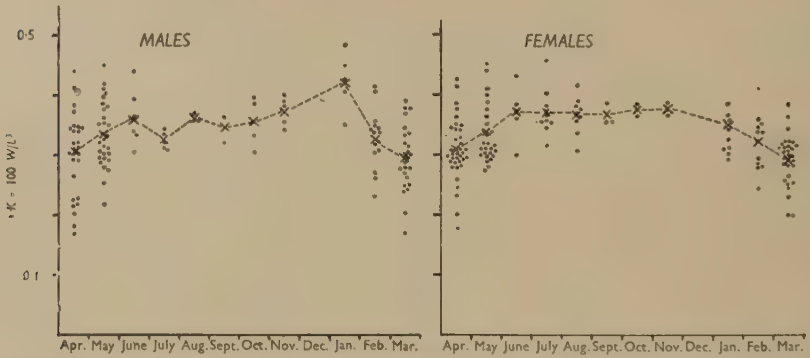


Fig. 5. Condition factor *K* in *Centronotus gunnellus*. Each point refers to an individual fish. X, gives the mean for each month.

FOOD

The gut contents of all the fish caught were examined and the various recognizable food items in each were listed. The occurrence of each category of food was then expressed as the percentage of the total number of fish examined which contained food of that category. As the samples available in each month were small, all the data obtained have been grouped into four quarters of the year. For instance, all the fish caught during the period from January to March of both years 1954 and 1955 were included in the first quarter. The percentage occurrence of various categories of food during each quarterly period is given in Table 6.

To determine the seasonal variation in the rate of feeding, the total food obtained from all the fish in each month was weighed after removing the excess of alcohol and water and expressed as the percentage of body weight of all the fish examined, including those which had empty guts. This pooling method minimized the contribution of the smaller fish to the results, but it had been found that their food was similar at least in quality to that of the larger fish. The weights of food found in the gut relative to the weight of fish for each month is shown as a histogram in Fig. 6. The histograms are divided vertically in a way which expresses the relative frequencies of occurrence in each month of the five most important classes of food, as judged by the percentage occurrence method. As can be seen from the figure, during January and February, which are the main breeding months, there occurs a marked reduction in the rate of feeding. The fish, which were guarding the eggs in these months, contained either no food or very little. In March the feeding intensity begins to rise. The majority of non-parents caught in this month contained food, but those still engaged in guarding the eggs showed little or no feeding (Table 5). In April and May the feeding intensity reaches a high level at which it remains until October. In November, when the gonads become large, the rate of feeding begins to diminish. It reaches its minimum during the breeding months. The rate of feeding determined by this method only tells the amounts of food present in the gut without taking into account the rate of digestion, but since the greater number of empty guts occurred during winter months, when the digestion is probably slower than it would be at the higher temperatures prevailing in summer, the deduction that the fish eat less during winter is reasonable.

Table 6. *Percentage occurrences of various categories of food in the gut during each quarterly period*

	Jan.-Mar.	Apr.-June	July-Sept.	Oct.-Nov.
Number of fish examined	85	130	31	15
Without food	31	10	1	3
Polychaeta	48·1	74·5	25·8	26·6
Amphipoda*	38·7	71·4	87·0	40·0
Isopoda	30·5	59·1	71·0	60·0
Decapoda	20·0	43·8	67·9	46·5
Copepoda	5·9	14·6	3·2	13·4
Caprella	5·9	6·9	–	6·7
Barnacles	16·4	32·3	19·4	53·1
Pycnogonida	8·2	10·8	3·2	13·4
Mite	2·3	3·8	–	–
Insect larvae	5·9	8·5	9·8	13·4
Gastropoda	13·0	22·4	12·9	13·4
Lamellibranchs	9·4	14·6	3·2	–
Algae	3·5	12·3	3·2	–
Hydrozoa	3·5	8·5	–	6·7
Ophiuroids	–	3·1	–	–
Sand and gravel	3·5	8·5	12·9	20·0
Unrecognizable food	4·7	9·2	22·5	6·7

* Amphipods not including *Caprella*.

A comparison of the relative proportions of the principal food organisms which occurred throughout the year, as shown in Fig. 6 and given in Table 6, on the quarterly basis, would indicate that there is a slight change in the food composition from season to season. From March to June, when the occurrence of polychaetes in the gut increases, there is a slight drop in the consumption of crustacean food such as amphipods, isopods, crabs, etc. In the following months, the fish seem to be feeding mostly on Crustacea and less on Polychaeta.

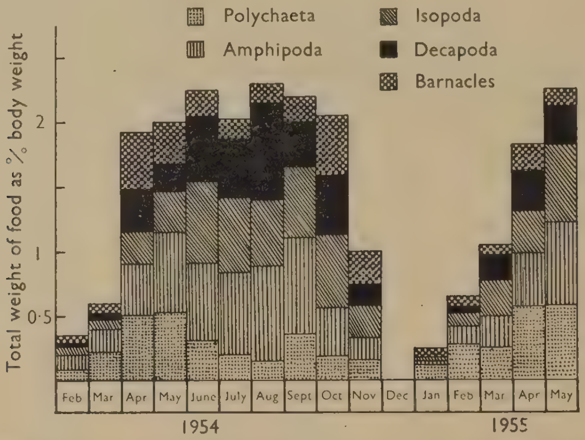


Fig. 6. Histograms showing the rate of feeding and the monthly variations in the composition of food. Only the five most important categories of food organism are shown, and the histograms are divided according to the relative percentage occurrences of these categories.

SUMMARY

1. Little information on age and growth in *Centronotus gunnellus* was obtained from seasonal analysis of length-frequency distribution. Each age-group determined from zones on the otoliths covered a large size range, but the average growth-rate is about the same in both sexes and goes on at a rather uniform rate throughout life.

2. Each female and most males spawn only once a year, during January and February. Eggs occur on the shore from January to March.

3. The regular cycle in the condition factor seems to be correlated with the seasonal changes in the gonads and loss of reserves during incubation. Maximum values were obtained just before spawning and minimum at the end of the breeding season.

4. The food consists of polychaetes, molluscs and a variety of crustaceans. There is a seasonal variation in the quantity of food consumed, with a maximum during spring and summer and a minimum in winter during the breeding season.

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THE DISTRIBUTION OF *ASELLUS* IN THE ENGLISH LAKE DISTRICT AND ADJOINING AREAS

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(With 1 Figure in the Text)

In a previous paper (Moon 1957), the distribution of *Asellus aquaticus* (L.) and *A. meridianus* Rac. in Windermere was described, and the suggestion made that, of the two species, *A. aquaticus* was a more recent arrival in the lake due to human agency, and that the two species were in competition. The present paper is an account of the distribution of *Asellus* in the Lake District and parts of its northern and southern borders. The approximate area covered is given in Fig. 1, and the types of habitat, together with the number of collections and different stations examined in each habitat, are given in Table 1. They are supported and confirmed by the very detailed information for the district, available at the Freshwater Biological Association's Windermere laboratory.

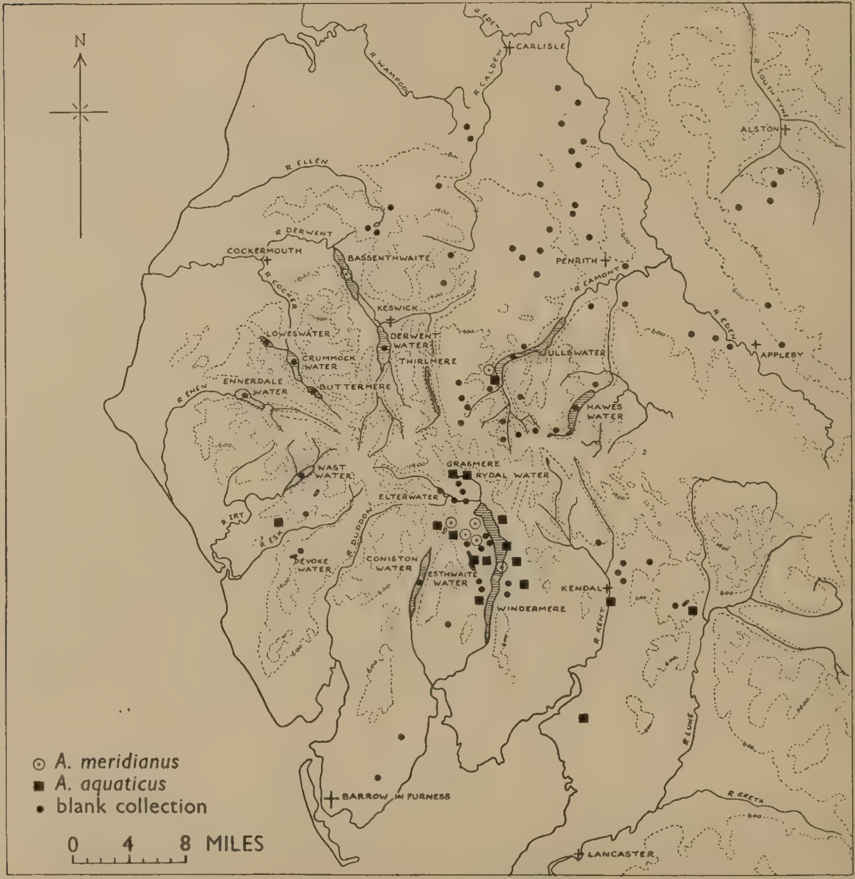
The collections were made between 1948 and 1956 with a large stramin hand net, and dredgings were made in Bassenthwaite, Esthwaite and Ullswater. In using the hand net the substratum was thoroughly disturbed, as *Asellus* often lurks in between the stones and in interstices of the gravel. The distinctions drawn in Table 1 between the various types of water body are quite arbitrary and serve to indicate the variety of habitats from which collections were made. A larger sheet of water occupying part of a valley at no great height and forming part of the drainage system was called a lake; tarns occupied the heads of valleys, often at considerable heights, while pools were shallow, often small, did not form part of the drainage system and occurred from the lowest to the highest levels of the fells.

RESULTS

As the larger lakes of the Lake District form a well-known group, the occurrence in them of *Asellus* is given separately in Table 2. Only five out of these fifteen lakes contain *Asellus*. Both species occur in Windermere, but only *aquaticus* is to be found in Esthwaite, Grasmere and Rydal, while in Bassenthwaite only *meridianus* occurs. In Rydal, *aquaticus* is scarce, and in Esthwaite earlier collections at various stations at various dates showed that it was absent. It has now been found at one of the stations where originally it was recorded as absent. This may imply recent introduction, or that originally it was very scarce at this station.

In Bassenthwaite, shore and dredge collections showed that only *meridianus* was present. This was checked along one stretch of coast line by a series of two-minute collections at 50 m intervals for 400 m, and then at 100 m intervals for another 400 m. No small pockets of *aquaticus* were found, as sometimes happened in Windermere on an otherwise purely *meridianus* shore.

Table 1 summarizes the results from all the habitats, and it is clear that *Asellus* is sparsely distributed, and was never found above 250 m. In places where it occurred in running water, it should be pointed out that, with the exception of the Rivers Bela and Kent, occurrences in streams were all immediately below standing water which contained *Asellus*. It was unusual to find both species in the same water body, but the two species occurred together in Tarn Hows and the adjoining Rose Castle Tarn. Both species are present in Windermere. Table 3 which lists the actual occurrences, emphasizes the sparse and scattered nature of the distribution.


N
R EDEN
CARLISLE
R WAMPOOL
R CALDEW
R SOUTH TYNE
ALSTON
R ELLEN
R DERWENT
COCKERMOUTH
R COCKER
BASSENTHWAITE
KESWICK
PENRITH
R EAMONT
LOWESWATER
CRUMMOCK WATER
DERWENT WATER
THIRLMERE
ULLSWATER
R EDEN
APPLEBY
ENNERDALE WATER
R EHEN
BUTTERMERE
HAWES WATER
WAST WATER
R IRT
R ESK
GRASMERE
RYDAL WATER
ELTERWATER
R DUDDON
DEVOKE WATER
CONISTON WATER
ESTHWAITE WATER
WINDERMERE
KENDAL
R KENT
R LUNE
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BARROW IN FURNESS
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600
1400
⊙ A. meridianus
■ A. aquaticus
• blank collection
0 4 8 MILES

Fig. 1. The occurrence of the two species of *Asellus* in the Lake District area.

DISCUSSION

In considering this distribution the same difficulty arises as in the case of Windermere, that there is no known feature of the environment with which a correlation can be made. The physical and chemical conditions of these waters are well known as a result of the work of the Freshwater Biological Association. It is, for example, quite impossible to account for the absence of *Asellus* from eleven of the fifteen lakes, since all these lakes offer habitats identical to those found in the lakes where the creature actually occurs. A further difficulty in trying to find an explanation for the distribution of the two species is the wide range of conditions which they can tolerate. Both can occur, for example, in clear running water on the one hand, and in organic ponds on the other, while *aquaticus* is a characteristic animal of fairly severe organic pollution.

Table 1. *Distribution of* Asellus *in the five main types of habitat. Windermere results are not included*

Habitat	Number of habitats examined	Number of stations	Number of collections	Occurrences of *Asellus*	
				aquaticus	*meridianus*
Lakes	14	207	342	3	1
Small lakes	9	35	51	3	–
Tarns	22	118	129	4	1
Pools	40	113	136	6	5
Becks, rivers	17	54	80	2	2
Total	102	527	738	18	9

Table 2. *Distribution of* Asellus *in the English Lakes*

	Species	Numbers of	
		Stations	Collections
Bassenthwaite	*Meridianus*	37	45
Brotherswater	None	4	4
Buttermere	None	14	22
Coniston	None	15	30
Crummock	None	24	35
Derwentwater	None	10	19
Ennerdale	None	18	43
Esthwaite	*Aquaticus*	6	14
Grasmere	*Aquaticus*	6	16
Haweswater	None	5	5
Loweswater	None	14	16
Rydal	*Aquaticus*	3	14
Ullswater	None	34	69
Wastwater	None	10	10
Windermere	Both	436	727

The absence of *Asellus* from high-level pools and tarns might be due to the more prolonged and rigorous winter conditions in these places. Another possible factor is the peaty character of high-level pools, but *Asellus* can occur in peaty water, as witnessed by its occurrence in a few pools around Tom Heights above Tarn Hows. Some of these high-level pools dry up in a hot summer, but the collections were made in pools known to survive periods of drought. The drying up of smaller intermediate pools would increase the difficulties of colonization for a creature such as *Asellus,* with no particular adaptations for dispersal.

Except for the actual outflows of bodies of water that contained *Asellus* it was very unusual to find it in running water in this district, although both species occur in fairly fast streams in the midlands and south of England. Many of the becks may well be too turbulent, particularly when in flood.

Table 3. *Details of the occurrences of* Asellus

Windermere, which contains both species, is not included in this table; *m, Asellus meridianus; a, A. aquaticus.*

Locality	Grid reference	Sodium (p.p.m.)	Habitat	Species
Bassenthwaite	35/219287	4·8	lake	*m*
River Bela	34/510798	5·7	river	*a*
Blelham Beck	34/372012	4·1	beck	*m*
Brathay Quarries (lower pools)	34/360017	3·9	pool	*m*
Cleabarrow	34/425964	6·2	pool	*a*
Crook	34/444956	3·5	pool	*m*
Drunken Duck	34/350011	–	pool	*m*
Drunken Duck Beck	34/350011	–	beck	*m*
Eskdale Green	34/145001	–	pool	*a*
Esthwaite Water	34/360968	4·6	lake	*a*
Grasmere	35/335065	3·5	lake	*a*
Green Hawes	34/363907	–	tarn	*a*
Hawkhowe Garden	35/387181	–	pool	*a*
Holmhowe Garden	35/387183	–	pool	*m*
River Kent Snuff Mills, Kendal	34/513904	–	river	*a*
Lilymere	34/604915	4·1	small lake	*a*
Middlerigg	34/399014	4·3	small lake	*a*
Rose Castle	34/335998	4·3	pool	*a m*
Scale Tarn (Claife)	34/374975	4·3	tarn	*a*
Tarn Hows	34/329998	4·0	tarn	*a m*
Rydal	35/355062	3·7	lake	*a*
Tom Heights	34/326003	–	pool	*a*
Tom Heights (north of)	34/328008	–	pool	*a*
Whinfell	34/558980	5·0	tarn	*a*
Wynandermere	34/592851	4·6	small lake	*a*

The problem of accounting for the sparse and random distribution of *Asellus* is only a particular aspect of the general question how freshwater bodies are colonized by plants and animals. As pointed out by Fritsch (1931), with reference to ponds, such habitats are as isolated as oceanic islands. Even where rivers or streams enter or leave bodies of fresh water, these rivers, by virtue of their speed and turbulence, may offer only poor facilities for distribution. Animals reaching areas of fresh water can do so by their own efforts as resistant eggs or stages, and also by attachment to other animals, or to plant material that is clinging to the limbs or bodies of larger animals such as aquatic birds. Evidence for this kind of thing was first given long ago by Darwin (1859, 1882), by Reid (1892), and has been recently reviewed by Talling (1951). Whatever the actual means of transport, it seems inevitable that the arrival of a freshwater animal or plant in a new habitat must be a matter of accident by virtue of the discontinuity of the habitat.

Asellus has no particular adaptation for distribution in either the adult or its life history, the young developing in a brood pouch and leaving it as virtually one-millimetre miniatures of their parents. As far as we can see, they must depend on some accidental means of dispersal into isolated and recent bodies of fresh water. Their normal means must be an infinitely slow advance through inter-connected water systems. In view of these facts, an explanation of the distribution is put forward, based on the idea that much of the distribution is accidental and results from the activities of man. In Table 4 the occurrences of *Asellus* are grouped according to whether the body of water in which they occur is natural or artificial. By artificial is meant such habitats as quarry pools, ornamental ponds, or streams dammed up to form small lakes or tarns for fishing or water supply. Some of these have been in existence for less than 30 years, the rest for not more than 100. They contain *Asellus*, while around them is a system of pools, lakes and streams which have been in existence for thousands of years and which contain no *Asellus*. Of the eight occurrences in naturally formed bodies of water, three consist of *A. aquaticus* only in Esthwaite Water, Grasmere and Rydal Water—all lakes with much residential and tourist activity along their shores. Windermere contains both species, but there is evidence that *aquaticus* is found on shorelines where residential activity is greatest. Bassenthwaite contains *meridianus* only. The three remaining water bodies of natural origin are fishing centres. The occurrence of *Asellus* in waters that are artificial, or whose shores are residential, is probably due to introduction on ornamental weeds, as fish food, debris from aquaria, live-bait cans, and perhaps most important of all, from the fish cans when fish have been introduced in stocking operations. It should be remembered that *Asellus* is one of the creatures recommended by aquarists and gardening journals as suitable for introduction into ponds and aquaria. It is easily transported in weed, and one gravid female can produce fifty or sixty young. Indeed one specimen in the laboratory produced 150 young.

Table 4. *Number of occurrences of* Asellus *in natural and artificial standing waters (including Windermere)*

	Natural	Artificial	Total examined
Lakes	5	–	15
Small lakes	–	3	9
Tarns	1	3	22
Pools	2	8	40
Total	8	14	86

As an actual example, the two occurrences of *Asellus* in the Ullswater district may be given. In one garden pond, stocked with weed from a dealer, *A. aquaticus* is present; in the other pond, stocked with water lilies from Sunderland, *meridianus* is present. The nearest known locality for *Asellus* is ten miles away over Kirkstone Pass. As a test, a small quantity of weed was ordered through the post from a dealer, and three *A. aquaticus* were collected from this sample.

The idea of accidental transport of freshwater faunas by man is not new, but is frequently neglected and requires emphasis. Kew (1893) gave much information relative to Mollusca; Macan (1950) suspects that the peculiar Molluscan fauna of School Knotts Tarn is due to aquarium debris. Hynes (1955) refers to the probable importance of fish-stocking, boating and canals on the distribution of *Gammaus pulex* in Great Britain.

The frequent occurrence of *Asellus* in very recent habitats and its absence from very ancient bodies of water is in interesting contrast to the results of Godwin (1923) and Elton (1927, 1929). Godwin found that, in a series of ponds of known age in the same district, the oldest ponds contained the richest flora. Elton found that *Diaptomus laciniatus* was usually only found in older bodies of water, its distribution being too slow to permit rapid colonization of more recent water bodies. Lowndes (1929) disputed the work on *Diaptomus* but his objections were dealt with by Elton. These are the kind of results which might be expected, and the fact that *Asellus* shows the reverse state of affairs, suggests the influence of some extraneous factor which would be uninfluenced by the age of a water body. Human activity might well be such a factor.

It remains to say something about Bassenthwaite which contains only *meridianus* and is a lake with very little residential or tourist activity. In the paper on the distribution of *Asellus* in Windermere, it was suggested that *meridianus* was the original species, but is now in competition with *aquaticus* which has been introduced later by human agency. On shorelines in Windermere where *aquaticus* is the dominant form, it occurs to the exclusion of *meridianus*, although below 60 cm, *meridianus* is the dominant species. The situation in Bassenthwaite may represent the state of affairs in a lake before the introduction of *aquaticus*, with *meridianus* equally abundant on the shoreline and in deeper water.

In conclusion, there is a point of general interest arising from this distribution: the almost complete absence of *Asellus* from the northern part of the area. Apart from the possibilities involving human agency, a geological factor may play a part here. The northern approaches to the Lake District are extremely dry, ponds being few and far between, owing to the belt of carboniferous limestone and the sandy rocks of the Permian and Triassic in the Vale of Eden. This produces very different country from the southern approaches, where the belt of carboniferous limestone is less continuous and thick deposits of drift produce wetter conditions.

SUMMARY

1. The occurrences of *Asellus aquaticus* and *A. meridianus* are sparse, and show no apparent correlation with any known physical or chemical factor of the environment.

2. The places where *Asellus* does occur are, with few exceptions, artificial and recent in origin, or places of tourist and residential activity.

3. It is suggested, therefore, that the distribution of *Asellus* in this area is largely due to human agency.

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THE DISTRIBUTION OF LUMBRICIDAE IN AN AREA OF PENNINE MOORLAND (MOOR HOUSE NATURE RESERVE)

By J. A. SVENDSEN

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Areas of Britain at altitudes approaching and above the tree line have a distinctive and reasonably well-known flora but their fauna is not known to the same extent. It was thought that the distribution of Lumbricidae in such an area might be limited and that a knowledge of any limitations would indicate some general requirements of the family and possible differences between species. To this end an investigation was made of the Nature Conservancy Reserve, N.R. 80, Moor House, situated in the northern Pennines approximately 11 miles (17·6 km) south of Alston, Cumberland. The Reserve is adjacent to and south-east of Cross Fell and the source of the River Tees and includes Great Dun, Little Dun and Knock Fells. The bulk of the area lies above 1800 ft (549 m); it has a characteristically cold, wet climate (Manley 1952) and is overlain with peat bog in various stages of decay and regeneration. Mull soils, generally accepted as the typical lumbricid habitat, are rare in extent, being restricted to the banks of streams and occasional limestone outcrops.

SPECIES LIST

Fifteen species of Lumbricidae were found at Moor House. Examples of these species are deposited at the British Museum and their registration numbers given with the following list:

	B.M. reg. no.
Lumbricus Linné:	
castaneus (Savigny)	1955:5:10:56-60
festivus (Savigny)	1955:5:10:61-65
rubellus Hoffmeister	1955:5:10:66-70
terrestris L.	1955:5:10:71-75
Allolobophora Eisen em. Rosa:	
caliginosa f. *typica* (Savigny)	1955:5:10:1-4
chlorotica (Savigny)	1955:5:10:31-35
terrestris f. *longa* (Ude)	1955:5:10:26-30
Dendrobaena Eisen em. Rosa:	
octaedra (Savigny)	1955:5:10:36-40
rubida (Savigny)	1955:5:10:15-19
Octolasium Oerley:	
cyaneum (Savigny)	1955:5:10:20-24
lacteum (Oerley)	1955:5:10:10-14
Eisenia Malm em. Michaelson:	
rosea mut. *macedonica* (Rosa)	1955:5:10:46-50
Eiseniella Michaelson:	
tetraedra f. *typica* (Savigny)	1955:5:10:41-45
tetraedra mut. *hercynia* (Michaelson)	1955:5:10:51-55
Bimastus Moore:	
eiseni (Levinsen)	1955:5:10:5-9

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With the exception of *Eisenia rosea* mut. *macedonica* and *Eiseniella tetraedra* mut. *hercynia* these are all species with a world-wide distribution so that thirteen of the seventeen peregrine species of the British fauna were found at Moor House. Species lists of Lumbricidae are not common for areas similar to Moor House. Forrest *et al.* (1929-36), in a survey of the Isle of Barra, found *Lumbricus terrestris, L. rubellus, Octolasium lacteum, Eisenia rosea, Bimastus eiseni, B. tenuis* (Eisen) and *Eiseniella tetraedra* f. *typica*. Backlund (1951) at between 650 and 1000 m altitude (2125-3270 ft) in Swedish Lapland recorded *Dendrobaena octaedra* and *D. subrubicunda* (Eisen). Both *Bimastus tenuis* and *Dendrobaena subrubicunda* may be synonyms of *Dendrobaena rubida* (Graff 1953) and if this is accepted then all the species found in these areas also occurred at Moor House.

LUMBRICID HABITATS RECOGNIZED AT MOOR HOUSE

Pearsall (1950) reviewed the major soil and vegetation types of British upland, and where possible some of the distinctions he made are used as 'habitats'. Thus habitat is employed here simply as a recognizably distinct area of vegetation or soil type.

(*a*) *Peat habitats*

The bulk of the Reserve is covered by a deposit of peat with a characteristic vegetation complex of *Calluna, Eriophorum* and *Sphagnum* species. This area is distinguished as moor and bog in the text but on occasion is subdivided into three types recognized by Pearsall (1950):

'*Eriophorum* moor' characterized by large expanses of naked peat with some *Eriophorum* sp. as the dominant plant;

'Bog moss' with *Calluna* and *Eriophorum* but characterized by an almost continuous cover of *Sphagnum* species; and

'*Calluna* moor' comprising drier areas with *Calluna* and *Cladonia* spp. and very little *Eriophorum* or *Sphagnum* spp.

A further predominantly peat habitat recognized, was between the deep peat of moor and bog and the mineral soils. This is distinguished as 'moor edge' and is characterized by the growth of *Juncus, Carex* and *Polytrichum* species.

(*b*) *Mineral soil habitats*

At Moor House the weathered rock material or 'drift' is so mixed that none of the soils can be said to have arisen from one rock type alone. The drift originally covered most if not all the area and may be seen underlying the peat in profiles cut by stream action. The following two habitats derived from exposed drift were recognized:

'Without raw humus': some of the drift overlying limestone, affected by the base rich rock, has produced clayey soils characterized by a rich flora and lack of raw humus in the soil profile.

'*Nardus* grassland' (Pearsall 1950): a mor type soil derived from either peat or drift and characteristic of some fell slopes.

Many streams dissect the Reserve and these invariably have banks of an alluvial deposit derived from the drift and peat. They exhibit a wide range of soil types dependent on the different proportions of these constituents. Areas of this type are summed by Pearsall (1950) as alluvial grassland but are here separated into four types recognized by their appearance:

'Without raw humus': a brown soil of fine texture. This habitat was not distinguished from the soils overlying limestone outcrops from which it was largely formed or influenced.

'Coarse alluvium': a grey, gritty soil from which the fine particles had been removed by stream action.

'Mixed alluvium': intermediate soils which could not be readily assigned to any of the other types.

'Redeposited peat': a black soil with a low mineral content.

(*c*) *Limnic habitats*

Parts of the stream beds were made up of raw alluvium which although very wet was never constantly and rarely completely immersed by the stream. Other limnic habitats occurred where there was some form of spring providing a constant but shallow flow of water.

METHODS

Habitats were investigated by digging and hand sorting soil cores (Svendsen 1955), by examining dung for contained worms and by searches of the soil surface and litter at night (Svendsen 1957). Two sizes of soil core, 1/25 and 1/35 sq. m, both 20 cm deep, were used. This method misses some of the deep burrowing forms, and underestimates could be expected of *Allolobophora terrestris* f. *longa* and *Lumbricus terrestris*. These species, however, were rare in the area studied; *Octolasium cyaneum*, on the other hand, was common and may also have been underestimated because of deep burrowing habits. With the possible exception of these species qualitative evidence supports Bornebusch (1930) in supposing that the bulk of Lumbricidae occur within the sample depth.

Fundamental differences of behaviour were observed between pigmented and unpigmented species of Lumbricidae (Svendsen 1957). These differences suggest that members of the pigmented species may be less dependent on soil type than those of unpigmented species and for this reason the two groups are, to some extent, treated separately.

RESULTS

(*a*) *Aggregation*

As a guide to the occurrence of aggregation, two sites of 1 sq. m were sampled completely by taking twenty-five adjacent soil samples. One site had a mixed alluvium soil, the other was of the without raw humus type. In both the relative position of each sample and the number of species of worm it contained was recorded. Since the samples were adjacent, the totals by species given in Table 1 are a representation in each case of the lumbricid population of 1 sq. m to a depth of 20 cm. To determine whether aggregation occurred, the numbers per species per sample were arranged in the spatial pattern in which they were found and their totals by blocks of five samples compared by χ^2. The distribution of *Octolasium cyaneum* from the without raw humus site is given in Table 2 as an example of this treatment. Aggregations of a similar order were shown to occur in the case of *Lumbricus rubellus*, *Allolobophora chlorotica* and *A. caliginosa*. Only *A. chlorotica* of the mixed alluvium site occurred in sufficient numbers to allow analysis by χ^2 as though the twenty-five samples had been randomized. The result failed to show aggregation, giving a χ^2 of 31·93, $P = 0{\cdot}15$. Satchell (1955*a*) demonstrated aggregation by several species and considered it to be a result of delayed spread following a period of rapid reproduction. An examination of the numbers of *A. chlorotica* from the mixed alluvium site does not support this view, since the aggregation appears to be restricted to the mature individuals. The horizontal and vertical blocks of the two groups are shown in Table 3 with the results of their analysis by χ^2. Active movement into dung has been demonstrated for the pigmented group of species, and in the unpigmented group high proportions of

Table 1. *Totals by species of two areas of 1 sq. m to a depth of 20 cm*

	Mixed alluvium	Without raw humus
PIGMENTED GROUP		
Lumbricus rubellus	49	79
L. festivus	2	64
L. terrestris	0	1
Dendrobaena rubida	14	24
Total	65	168
Weight (g)*	6·4	28·5
UNPIGMENTED GROUP		
Octolasium cyaneum	28	83
Allolobophora chlorotica	241	6
A. caliginosa	54	93
A. terrestris	0	38
Eisenia rosea	81	1
Total numbers	405	221
Weight (g)*	43·6	81·4
Total numbers of both groups	470	389
Total weight (g)*	52·0	109·9

* Preserved worms (4% Formalin) were dipped in 70% alcohol, surface dried and then weighed.

Table 2. *The distribution of* Octolasium cyaneum *throughout 1 sq. m of without raw humus soil*

						Totals
	2	0	1	2	0	5
	2	0	2	1	2	7
	7	2	1	6	4	20
	8	5	4	6	3	26
	3	11	2	3	6	25
Total	22	18	10	18	15	83

Horizontal block $\chi^2 = 23{\cdot}93$, $P = 0{\cdot}001$

Vertical block $\chi^2 = 4{\cdot}77$, $P = 0{\cdot}30$

mature to immature specimens were active at night and also aggregated near dung (Svendsen 1957). It seems, therefore, that Lumbricidae are sufficiently active to develop aggregations as a result of slower movement through favourable localities.

Table 3. *A comparison of the distribution of mature and immature specimens of* Allolobophora chlorotica

	Mature specimens		Immature specimens	
	Horizontal blocks	Vertical blocks	Horizontal blocks	Vertical blocks
Σ1	14	36	43	37
Σ2	14	15	37	25
Σ3	18	14	22	33
Σ4	19	6	27	31
Σ5	16	10	31	34
$\chi^2 =$	1·28	33·38	8·5	2·5
$P =$	0·85	0·001	0·07	0·60

(*b*) *The numbers of Lumbricidae in alluvial soils*

Fifty-three sites along the banks of three streams were sampled twice by cores of 1 25 sq. m surface area in the summer of 1952. These sites covered a number of each of the alluvial soil types, but neither their number nor the number of samples per site was sufficiently great to allow detailed analysis; nevertheless, as Table 4 shows, certain differences existed. In as far as one associates a deterioration in soil

Table 4. *The proportion of sites in which each species was found, and the mean number of each species per site*

	Without raw humus (8 sites)		Mixed alluvium (28 sites)		Coarse alluvium (5 sites)		Redeposited peat (12 sites)	
	Sites with species	Mean per site	Sites with species	Mean per site	Sites with species	Mean per site	Sites with species	Mean per site
PIGMENTED GROUP								
Lumbricus festivus	0·50	1·88	0·07	0·11	–	–	–	–
L. rubellus	0·88	4·00	0·58	1·71	0·80	3·40	0·58	1·33
Dendrobaena octaedra	0·13	0·13	0·11	0·39	0·40	0·60	0·25	0·42
D. rubida	0·50	0·50	0·64	1·50	0·60	1·20	0·58	5·00
Total	2·01	4·51	1·40	3·71	1·80	5·20	1·41	6·75
Weight (g)*		1·38		0·58		1·30		0·54
UNPIGMENTED GROUP								
Allolobophora chlorotica	0·88	8·13	0·93	14·44	0·80	11·80	0·25	2·42
A. caliginosa	0·88	7·97	0·50	4·32	–	–	–	–
A. terrestris	0·25	0·63	0·04	0·04	–	–	–	–
Eisenia rosea	0·50	0·97	0·32	2·46	0·20	0·40	0·08	0·17
Octolasium cyaneum	0·75	3·75	0·50	1·71	0·80	3·40	–	–
O. lacteum	–	–	0·18	0·96	–	–	–	–
Total	3·26	21·45	2·47	23·93	1·8	15·6	0·33	2·59
Weight (g)*		5·39		3·69		3·71		0·40
Weight (g)* both groups		6·77		4·27		5·01		0·94

* Preserved worms (4% Formalin). See footnote to Table 1.

quality with a change from mull to mor type humus, Bornebusch's (1930) suggestion, that 'the total weight of animals in deciduous forest soil gradually falls in proportion to the deterioration in soil quality' may be applied to the present data. The difference between redeposited peat and without raw humus soils shown in Table 4 is clear; in both pigmented and unpigmented species there is a drop in weight from the mull to the mor type of soil. Such a decrease in weight, however, was not always accompanied by a decrease in numbers, indeed there is some evidence that between without raw humus and mixed alluvium the reverse was the case. This is also shown in Table 1, where 470 worms weighed 52·0 g while 389 weighed 109·9 g, it is even more striking when only the unpigmented species are considered, since 405 worms weighed 43·6 g while 221 weighed 81·4 g. These differences arose from a change in species composition and not from a change of weight within species.

(*c*) *Dung associated species*

Of the Lumbricidae which are surface active and habitually aggregate in dung (Svendsen 1957) four species were common at Moor House, *Lumbricus rubellus*, *Dendrobaena rubida*, *D. octaedra* and *Bimastus eiseni*. All these species are deeply pigmented, a character which appears to be correlated with surface activity (Bornebusch 1930, Svendsen 1957). The proportions of these species found in dung from three important habitats, moor and bog, alluvial grassland and moor edge are given in Table 5. Since neither the habitat areas nor the number of pieces of dung from which the worms were obtained were constant, only the species proportions are considered. It appears that *Dendrobaena octaedra* and *Bimastus eiseni* form the bulk of the Lumbricidae of moor and bog, giving way to *Dendrobaena rubida* and *Lumbricus rubellus* on better soils.

Table 5. *Percentages of four species found in dung from three habitats*

	Alluvial grassland	Moor edge	Moor and bog
Number of habitat sites examined	15	6	15
Total number of worms	2784	670	417
Lumbricus rubellus	57	28	1
Dendrobaena rubida	35	39	0
D. octaedra	7	27	50
Bimastus eiseni	1	6	49

Differences within the moor and bog habitat, *Eriophorum* moor, Bog moss and *Calluna* moor were investigated by a quantitative search of naturally occurring dung in September 1954. Twenty-five randomized sample areas, each 25 × 2 m, were taken on all three habitats, and for every sample the number of pieces of dung found and the number of worms per piece were recorded. Species were only recorded for the total collection from each habitat. Table 6 shows that no difference occurred between the proportions of *Dendrobaena octaedra* and *Bimastus eiseni* for the three habitats, and therefore in the following analysis these two species are considered together. Two sources of error may have influenced these results; dung may have been missed, and the length of time it had been liable to invasion could not be assessed. The probability of finding dung was greater with decreased vegetation (*Eriophorum* moor), and by not being eaten pieces of dung would tend to survive longer in areas of low lumbricid populations (*Eriophorum* moor). In terms of total available dung, therefore, the errors would, if operative, have minimized the differences observed. Thus there was more dung available for the 300 Lumbricidae on the drier *Calluna* moor (216 pieces) and less for the 104 of the wetter *Eriophorum* moor (96 pieces). The proportions of invaded dung differed between the areas, being 7·7%, 21·4% and 28% respectively. Analysis of these proportions by a contingency table, the first part of Table 6, shows them to be significantly different, $\chi^2 = 18{\cdot}39$, $P = 0{\cdot}001$; thus the number of Lumbricidae invading dung on naked peat was less than that on areas dominated by *Calluna*.

Table 6. *Pieces of dung and their contained worms from 1250 sq. m of three peat habitats*

	Dung without worms	Dung with worms	Total dung	*Dendrobaena octaedra*	*Bimastus eiseni*	Total worms
Eriophorum moor	96	8	104	3	7	10
Bog moss	99	27	126	29	20	49
Calluna moor	216	84	300	58	77	135
Total	411	119	530	90	104	194

The total amount of dung found on any area was not necessarily a true measure of the amount available for the Lumbricidae; dung could be too fresh to allow invasion, and it is probable that it could also lose attractiveness with age. A total of 194 worms were found in 119 pieces of dung over the area as a whole, representing 1·63 worms per piece which could be assumed attractive; the expected totals based on this mean are compared with the observed in Table 7. Thus measured only by the dung invaded the number of worms in each habitat was as expected.

Table 7. *Observed and expected numbers of worms in pieces of dung*

	Eriophorum moor	Bog moss	*Calluna* moor	Total
Observed	10	49	135	194
Expected	13	44	137	194
χ^2	0·71	0·57	0·03	1·31
$P = 0{\cdot}50$				

This may have been either because the proportions of suitable dung differed in the three habitats, or because only parts of each and these in different amounts provided a suitable environment for Lumbricidae. It is not possible with the evidence available to separate these factors, but it seems probable, judged by either the number of worms or species, that moor and bog is an environment at the extreme of the lumbricid range. It is therefore likely that the results reflected the proportions of each habitat which provided a suitable environment even for *Dendrobaena octaedra* and *Bimastus eiseni*.

A series of experiments designed to investigate the behaviour which led pigmented Lumbricidae to invade dung, were made in 1953 and 1954 (Svendsen 1957). Of these one provided some information on the distribution of dung-associated species in different alluvial habitats. In this case six sites were treated similarly by laying down prepared pieces of dung, and their contained worms were collected daily for a period of sixteen days. One site was on moor edge, one on without raw humus, and four on mixed alluvium, of which one was distinct from the others in that its vegetation was rank and comparatively little grazed. The totals of worms collected from the dung of these sites were directly comparable and are given in Table 8. The area of influence of the dung was unknown but is assumed to have been the same in each case. The moor edge site differed from the others in containing *Bimastus eiseni* and in having a low total of worms of all species. The without raw humus site was characterized by *Lumbricus castaneus* and a high total. Of the mixed alluvium sites nos. 3 and 4 were similar, while no. 1 differed from them in having a high number of *Dendrobaena octaedra* and no. 2 in having a low number of *D. rubida*. *Lumbricus rubellus* and *Dendrobaena rubida* could apparently live in all of these habitats but were more numerous under mull conditions. *Lumbricus castaneus* and *L. festivus* may have been restricted to mull conditions while *Dendrobaena octaedra* and *Bimastus eiseni* tended towards mor type soils.

Table 8. *Worms collected from pieces of dung laid down on different sites*

	Without raw humus	Mixed alluvium				Moor edge
		1*	2	3	4	
Lumbricus festivus	4	4	3	–	1	–
L. castaneus	35	–	–	–	–	–
L. rubellus	247†	166†	190†	258	219†	52
Dendrobaena rubida	152	115	34	117	137	53
D. octaedra	2	55	12	7	15	9
Bimastus eiseni	–	–	–	1	–	13
Total	440	340	239	383	372	127

* Rank, little grazed vegetation.

† Contained a proportion of the other *Lumbricus* species present.

(*d*) *The occurrence of two species outside the range of soil or dung-sampling methods*

Lumbricus terrestris. Night searches of a restricted area (within 200 m of the house, altitude 1825 ft (556 m) showed *L. terrestris* to be common in deep mull soils. This species occurred only once in soil samples but may have been underestimated by this method as it does not aggregate in dung; since the area where it was found by night searches was restricted, it is possible that it was more widespread than the lack of records suggest.

Eiseniella tetraedra f. *typica* and mut. *hercynia*. *E. tetraedra* was found mainly during random searches of stream beds and flushes which may be considered its typical habitat. On occasion, however, it occurred away from free water, and was once found in appreciable numbers in dung on *Nardus* grassland. Guild (1951) has also recorded this species away from free water on a slope of 'rough pasture'.

DISCUSSION

The extraction of a known quantity of soil and the removal of Lumbricidae to give an estimate of numbers has been practiced since the mid-nineteenth century (Hensen 1877). More recently chemical (Evans & Guild 1947) and electrical (Satchell 1955*b*) vermifuges have been employed. The results obtained by these and other workers vary tremendously even for similar soils, so that it is difficult to suggest an average with which the Moor House figures can be compared. Some of the variation, however, may have been due to sampling method (Svendsen 1955) and this is thought to explain the high numbers found at Moor House (Table 1, 389 and 470 per sq. m) which might otherwise be contrasted with smaller numbers obtained by other authors under lowland conditions.

As a group of soil-living animals Lumbricidae are of special interest because of their supposed effects on topsoil formation and maintenance (Darwin 1881, Crompton 1953). Müller (1878) demonstrated that different species of Lumbricidae were typical of different soil types and outstanding among others, Bornebusch (1930) confirmed and amplified his findings. Guild (1948) showed differences between species complexes and their numbers, which were associated with the mechanical properties of soil types. The importance of arable farming in reducing lumbricid numbers by lowering soil temperatures and water content was demonstrated by Evans & Guild (1947, 1948) while Krüger (1952) considered the reduction followed from the mechanical disturbance. In discussing the distribution of lumbricid populations Guild (1951) suggested that soil acidity reduced both numbers and species, while he also considered (1952) low soil water content to produce the same result. A positive correlation between numbers and the calcium content of the soil was demonstrated by Nielson (1951); conversely, Satchell (1955*a*) considered pH to be more important than calcium deficiency in controlling lumbricid distribution.

At Moor House, the factors listed above were not directly investigated. The habitats distinguished, however, clearly covered a wide range of soil conditions such as mechanical properties, pH, calcium and water content. The presence of Lumbricidae in all habitats suggests that the family has a wide range of requirements, but there was no evidence that any one species could live equally well in all habitats.

A number of behavioural differences between species are known. Bornebusch (1930) suggested three distinct zonations of activity: surface litter forms, surface to 20 cm, and deep-burrowing forms. Evans & Guild (1947) showed that only a few species produce surface casts, and that while some species periodically and obligatorily aestivate, others do not. It has been known for some time that 'earthworms' sometimes feed on the surface at night while retaining their 'tail' within a burrow (Darwin 1881); at Moor House this habit was restricted to one species, *Lumbricus terrestris* (Svendsen 1957). Again at Moor House surface activity leading to aggregation in dung was limited to the deeply pigmented species. It is thought that these behavioural differences suggest different requirements; for example, whereas small climatic changes were important to surface active forms (Svendsen 1957), they would hardly affect the deeper soil dwellers to the same extent.

Bodenheimer (1935) reviewed the conditions which limit earthworm distribution and suggested that the requirements of different species would prove to be too varied to allow any one overall controlling factor to be discovered. The present writer agrees.

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SUMMARY

1. Fifteen species of Lumbricidae were found within an area of Pennine upland, the Nature Conservancy Reserve, Moor House. Of these, four pigmented species, *Lumbricus rubellus* Hoffmeister, *Dendrobaena rubida* (Savigny), *D. octaedra* (Savigny) and *Bimastus eiseni* (Levinsen), and four unpigmented species, *Allolobophora chlorotica* (Savigny), *A. caliginosa* (Savigny), *Octolasium cyaneum* (Savigny) and *Eisenia rosea* mut. *macedonica* (Rosa), were common.

2. Lumbricid aggregations within areas of 1 sq. m were shown to occur, and were thought to result from the active movement of individuals.

3. Four alluvial soil habitats, 'without raw humus', 'mixed alluvium', 'coarse alluvium' and 'redeposited peat', showed most species, and the greatest weight of Lumbricidae occurred in without raw humus and the least in redeposited peat. The greatest numbers in any habitat were not necessarily associated with the greatest weight.

4. The proportions of the four common dung-associated species were found to vary. *Lumbricus rubellus* and *Dendrobaena rubida* were typical of alluvial soils, and *D. octaedra* and *Bimastus eiseni* of moor and bog, while all four met under moor edge conditions.

5. The dung-associated species found in the dung on alluvial habitats followed a similar pattern to the soil-living species, in that dung on without raw humus areas contained more species in greater numbers than that on other areas.

6. A detailed investigation of the numbers of *Dendrobaena octaedra* and *Bimastus eiseni* in the dung of moor and bog suggested that only parts of this area provided a suitable environment even for these species.

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THE BEHAVIOUR OF LUMBRICIDS UNDER MOORLAND CONDITIONS

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(With 3 Figures in the Text)

The observations described here formed part of a study of the Lumbricidae of an area of the northern Pennines, the Nature Conservancy Reserve, Moor House. Most of this area is covered by peat bog, but mineral soils occur as alluvial deposits forming the banks of streams, and comparatively base rich soils overlying limestone outcrops. Throughout the summer the Reserve was grazed by sheep and their dung was frequent on both the peat and mineral soils. The general distribution of Lumbricidae at Moor House is described elsewhere (Svendsen 1957) while the present paper is concerned with differences of behaviour between the species.

PART I. BEHAVIOUR OF WORMS ASSOCIATED WITH DUNG

Lumbricidae are well-known inhabitants of dung, and for at least one species, *Eisenia foetida* (Savigny), manure and compost heaps are given as a typical habitat (Cernosvitov & Evans 1947). *E. foetida* did not occur at Moor House but a number of other species were common in the dung of the area. Two species, *Bimastus eiseni* (Levinsen) and *Dendrobaena octaedra* (Savigny), were found in the dung of the peat bog, and others, notably *Lumbricus rubellus* Hoffmeister and *Dendrobaena rubida* (Savigny), in the dung of the mineral soils. In both cases the number of worms in dung were greater than would have been expected had they only entered from the immediately adjacent soil. It appeared, therefore, that some aggregation into dung occurred, and a field experiment was designed to demonstrate the aggregation, the species concerned, and to what extent if any the dung was sought. Lumbricidae may be subdivided into pigmented and unpigmented groups of species, and at Moor House seven pigmented and eight unpigmented were found. The pigmented group included the four given above and three other *Lumbricus* species, *L. castaneus* (Savigny), *L. festivus* (Savigny) and *L. terrestris* L. The unpigmented group was made up of two *Octolasium* species, *O. cyaneum* (Savigny) and *O. lacteum* (Oerley), three *Allolobophora* species, *A. caliginosa* (Savigny), *A. chlorotica* (Savigny) and *A. terrestris* f. *longa* (Ude), *Eisenia rosea* mut. *macedonica* and two forms of *Eiseniella tetraedra*, f. *typica* (Savigny) and mut. *hercynia* (Michaelson).

METHODS

Pieces of dung were laid an equal distance apart and a series of treatments designed by which either entrance to dung or its flow of products was controlled. The worms' entrance to dung was restricted from beneath by a gauze plate and from the surface by a gauze ring. A further restriction of surface entry in the form of an artificial surround was provided by placing dung on the surface of tiles. The effect of dung products was assessed by a comparison of worm numbers from beneath tiles with and without dung on their surfaces. Again the possibility of perception of dung products was reduced in some cases by laying dung on funnels arranged to carry any solutions produced by rain deep into the soil. The importance of dung volume was shown by a comparison of worm numbers obtained from a standard volume dung with those from half and twice the standard.

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Two series of trials were made, at one site in 1953 and at six in 1954. Since, for the purpose of the experiment large numbers of worms were required, selected sites had high earthworm populations. The soil type of the sites and the significance of differences in the species proportions between sites are discussed elsewhere (Svendsen 1957). At the beginning of a trial the dung was made homogeneous by thorough bulk mixing. Unless otherwise stated, pieces of dung 300 ml in volume were used for all treatments. The treatment positions were 1 m apart and were examined daily for the period of each trial. Details of the trials and treatments are given below.

1953—A pilot trial of seven treatments was examined for one period of 14 days. The seven treatments were:

1. A control of 300 ml of dung placed on the ground. (Normal dung, N, 5 replications.)
2. Dung placed on top of a floor tile, 15 cm square and 2 cm thick. (Dung on tile, T +, 5 replications.)
3. The surface of the soil immediately beneath the tile with dung on top. (Beneath tile with dung on top, T –, 5 replications.)
4. Dung laid on a phosphor bronze gauze plate (1 mm mesh) 10 cm in diameter. The dung completely covered the gauze plate. (Gauze plate, G, 5 replications.)
5. The surface of the soil immediately beneath a tile without dung. (Beneath tile without dung, T, 5 replications.)
6. Dung laid on a gauze plate over a funnel of 10 cm diameter sunk flush with the ground. The stem of the funnel was extended by first sinking a length of pipe making the effective outlet more than 20 cm deep. (Funnel, F, 3 replications.)
7. Dung laid inside a gauze ring of 10 cm diameter. The ring was sunk into the ground 2 cm and extended above the surface 10 cm.

1954—For three periods of 15, 7 and 2 days in June, September and October 1954 the experiment was repeated on six sites with three replications of eleven treatments. The treatments modified and added to the 1953 experiment are detailed:

1. Normal dung (N) as for 1953.
2. Half normal dung ($\frac{1}{2}$N) 150 ml of dung.
3. Twice normal dung (2 N) 600 ml of dung.

4. Dung on tile (T+) as for 1953.
5. Beneath tile plus dung (T−) as for 1953.
6. Beneath tile without dung (T) as for 1953.
7. As for dung on tile T+ but with 4 cm deep strip of perforated zinc surrounding the tile, sunk 2 cm into the ground and not extending above the tile surface (GT+).
8. As for T−, but the area beneath the tile and within the zinc strip of GT+ (GT−).
9. Dung placed on a plate of perforated zinc over a funnel sunk flush with the ground, the end of the funnel being blocked with soil. The funnel and plate were 15 cm in diameter and the dung did not therefore reach the edge. Gauze plate (G).
10. Funnel (F) as for 1953 but with a 15 cm diameter funnel and a perforated zinc plate.
11. Ring (R) as for 1953 but of perforated zinc and a diameter of 15 cm.

RESULTS

The totals by species for the seven treatments of the 1953 pilot trial are given in Table 1. Since there were only three replications of treatment F compared with five of the others, the totals for F have been multiplied by 1·4 for ease of comparison. The total number of worms obtained, in three trials of eleven treatments and three replications from each of six sites used in 1954, is given in Table 2. The total number of each species from each of these sites is given in Table 3.

Table 1. *Totals by species for treatments of 1953 pilot trial*

	Treatments							
PIGMENTED GROUP	N	T−	T+	T	G	R	F	Total
Lumbricus rubellus	104	87	25	7	95	22	50	390
L. festivus	4	4	–	–	–	1	–	9
Dendrobaena octaedra	3	–	–	–	2	–	1	6
D. rubida	25	16	–	–	26	20	6	93
Total	136	107	25	7	123	43	57	498
UNPIGMENTED GROUP								
Octolasium cyaneum	–	1	–	–	–	–	–	1
Allolobophora chlorotica	2	8	–	1	1	15	–	27
A. caliginosa	1	4	–	–	–	2	–	7
Eisenia rosea	1	1	–	–	–	–	–	2
Eiseniella tetraedra	2	–	–	–	1	–	1	4
Total	6	14	–	1	2	17	1	41
Total both groups	142	121	25	8	125	60	58	539

(*a*) *The effect of the sites and replications on the treatments*

Items $= x$; Eleven treatments $= a$; Six sites $= b$; Three replications $= c$; Sum of number per replication $= R$; Sum of number per site $= S$; Sum of number per treatment per site $= t$; Sum of number per treatment $= T$; Sum of items $= G$;

Table 2. *The Lumbricidae from the treatments and replications of six experimental sites—1954*

Replications	Treatments											
	N	T−	T+	½N	GT−	GT+	2N	T	G	F	R	Total
1	25	9	10	10	9	4	77	2	4	4	29	183
2	52	20	12	10	17	8	28	–	4	–	3	154
3	20	46	1	19	14	7	56	9	8	7	4	191
1	26	20	6	5	23	2	47	11	5	4	2	151
2	33	22	4	15	18	10	47	6	12	–	6	173
3	44	39	5	18	31	6	40	2	5	2	3	195
1	37	21	6	21	8	1	19	6	7	7	17	150
2	51	35	20	83	58	31	153	32	43	1	11	518
3	54	57	19	27	41	13	100	19	14	6	5	355
1	5	4	3	6	11	2	11	–	3	–	6	51
2	9	10	1	5	–	4	34	2	4	1	3	73
3	6	2	6	9	22	10	62	13	9	3	4	146
1	20	11	9	8	8	12	41	2	11	6	10	138
2	35	5	17	9	11	18	48	1	28	8	6	186
3	33	11	8	11	15	22	47	2	11	7	7	174
1	50	17	12	17	16	7	79	4	14	2	5	223
2	37	25	32	27	25	13	64	11	21	4	8	267
3	45	24	2	21	15	13	85	4	18	3	5	235
Total	582	378	173	321	342	183	1038	126	221	65	134	3563

Table 3. *Total by species of six 1954 experiental sites*

	Sites					
PIGMENTED GROUP	1	2	3	4	5	6
Lumbricus festivus	13	5	5	–	8	–
L. castaneus	66	–	–	–	–	–
L. rubellus	593*	227*	363*	322	416*	129
Dendrobaena rubida	281	151	63	151	202	111
D. octaedra	3	61	24	10	35	11
Bimastus eiseni	1	–	–	1	–	19
Total	957	444	455	484	661	270
UNPIGMENTED GROUP						
Allolobophora caliginosa	15	9	–	–	–	–
A. chlorotica	45	72	59	13	56	–
A. terrestris	1	–	2	–	–	–
Octolasium cyaneum	1	1	3	–	1	–
Eisenia rosea	4	2	–	–	7	–
Eiseniella tetraedra	–	–	–	1	–	–
Total	66	84	64	14	64	–
Total both groups	1023	528	519	498	725	270

* Contains a proportion of the other *Lumbricus* species.

Then:

$$\text{Correction} = \frac{G^2}{abc} = 64116\cdot 00$$

$$\Sigma_1 = \frac{S^2_1 + S^2_2 \text{ .... } S^2_6}{ac} - \text{Correction} = 9859\cdot 85$$

$$\Sigma_2 = R_{1,1} + R_{1,2} \ldots\ldots R_{6,3} - \text{Correction} = 16856\cdot 27$$

$$\Sigma_3 = \frac{(R_{1,1} + R_{2,1} + R_{3,1} \ \ldots\ldots)^2 + \ldots\ldots + (\ldots\ldots + R_{5,3} + R_{6,3})^2}{ab}$$

$$-\text{Correction} = 1976\cdot 01$$

$$\text{Error} = \Sigma_1 - \Sigma_3 = 5020\cdot 41$$

	Sum of squares	d.f.	Mean of squares	F
Between sites	9859·85	5	1971·97	3·92
Between replications	1976·01	2	988·01	1·90
Error	5020·41	10	502·04	
Total	16856·27	17		

Since there is no significant effect on the treatments by either the sites or the replications, they may be summed and the analysis continued.

(*b*) *Differences between treatments*

$$\Sigma_4 = \frac{T^2_1 + \text{ .... } + T^2_{11}}{bc} - \text{Correction} = 43071\cdot 39$$

$$\Sigma_5 = t^2_{1,1} + t^2_{1,2} + \ldots\ldots + t^2_{6,10} + t^2_{6,11} - \text{Correction} = 61569\cdot 67$$

$$\Sigma_6 = \Sigma_5 - \Sigma_4 - \Sigma_1 = 8638\cdot 43$$

$$\Sigma_7 = \Sigma x^2 - \text{Correction} = 84106\cdot 00$$

$$\text{Error} = \Sigma_7 - \Sigma_6 - \Sigma_4 - \Sigma_2 = 15539\cdot 91$$

	Sum of squares	d.f.	Mean of squares	F
Whole block	16856·27	17		
Between treatments	43071·39	10	4307·14	33·26
Sites × treatments	8638·43	50	172·77	1·33
Error	15539·91	120	129·50	
Total	84106·00	197		

The difference between treatments is highly significant and may be examined by the standard error of the treatment means which equals:

$$\frac{\sqrt{129{\cdot}5}}{9} = 3{\cdot}794$$

The treatment means are:

Normal dung	N	582÷18	= 32·33
Beneath tile plus dung	T−	378	= 21·00
Dung on top of tile	T+	173	= 9·61
Half normal dung	½N	321	= 17·83
Beneath tile with gauze ring plus dung	GT−	342	= 19·00
Dung on tile with gauze ring	GT+	183	= 10·17
Twice normal dung	2N	1038	= 57·66
Beneath tile without dung	T	126	= 7·00
Gauze plate	G	221	= 12·28
Funnel	F	65	= 3·61
Ring	R	134	= 7·44

(c) *The effects of some treatments on the proportions of mature and immature specimens found*

The proportion of mature animals per treatment was examined by analysis of variance for the five treatments, N, ½N, 2N, T− and T+ with the following result:

	Sum of squares	d.f.	Mean of squares	*F*
Between sites	·3229	5	·0645800	5·82
Between treatments	·4667	4	·1166750	10·52
Residual	·221752	20	·0110876	
Total	1·011352	29		

There is a significant difference between the treatments. The treatment means and their standard error are shown:

Normal dung	N	= ·2912
Beneath tile plus dung	T−	= ·5468
Dung on tile	T+	= ·1750
Half normal dung	½N	= ·2528
Twice normal dung	2N	= ·3147

Standard error = ·01924

(*d*) *The effect of some treatments on the proportions of four common species found*

The proportions of four species, *Lumbricus rubellus*, *Dendrobaena octaedra*, *D. rubida* and *Allolobophora chlorotica* found by the treatments N, T−, T+, ½N, 2N and R were examined for each site by contingency tables. An example of the results is given in Table 4 derived from the sum of three similar sites, 2, 3 and 5 of the 1954 trials. This demonstrates that the four species did not respond similarly to all treatments.

DISCUSSION

Six pigmented and six unpigmented species were found in the 1954 trials and of 3563 worms, only 8·2% belonged to the unpigmented group of species. Clearly the numbers of any species found depended on their proportion available in the surrounding area. Soil samples from areas similar to those of the trials were taken and are discussed elsewhere (Svendsen 1957). For comparison the percentage of each species found by soil samples and dung trials is given in Table 5 which shows a marked increase in the proportion of pigmented species for the dung trials. Since the trials total includes those worms from the treatments 'beneath tiles' where some unpigmented species could be expected, it is concluded that the unpigmented species are relatively inactive in aggregating in dung.

Treatments ½N, N and 2N differed in their dung volume being, 150, 300 and 600 ml respectively. The number of worms were directly related to dung volume—a mean of 57·7 worms for 600 ml, 32·3 for 300 and 17·8 for 150 ml. Since worms were removed from the dung daily these differences can hardly have been produced by crowding. Again although the ground surface covered by the dung increased with amount, it is unlikely that this slight increase could account for the differences observed. No difference was found in either the species proportions or the proportions of mature forms between these three treatments, and it seems that the larger volumes of dung were more attractive to all species and states than the smaller volumes. The reason is obscure. It is possible that the larger volumes modified the effects of fluctuations in the external environment (temperature and water loss) and the twice normal volume may therefore have been most attractive because of the conditions existing during the period of the trials.

Table 4. *Table of χ^2 from a contingency table of species proportions*

Significant χ^2s as a result of a lower observed proportion than expected are in heavy type while those from too high a proportion are in italics.

	Treatments						
	N	T−	T+	½N	2N	R	Total
Lumbricus rubellus	1·07	2·20	4·41	1·99	0·01	**14·11**	23·79
Dendrobaena octaedra	3·76	2·73	0·49	0·20	0·02	0·10	7·30
D. rubida	1·34	1·21	0·72	3·00	1·30	*24·36*	31·93
Allolobophora chlorotica	**5·41**	*43·54*	8·78	0·05	2·08	0·72	60·58
Total	11·58	49·68	14·40	5·24	3·41	39·29	123·60

The aggregation into dung of some lumbricid species indicates that it is an attractive habitat. The greater number of worms found under the 'tile with dung' compared with its control 'tile without dung' (treatment means T−, 21·0 : T, 7·0) suggests that the worms responded to the dung products alone. Similarly, smaller numbers of worms were obtained from the dung of treatment F, 'dung on funnel', where the products were carried deep into the soil than from its control G, 'dung on gauze plate', where more of the products remained on the surface (treatment means F, 3·6 : G, 12·3).

There was no significant difference between the numbers of worms obtained from the treatments, tile plus dung (T− and T+) and the tile with gauze plus dung (GT− and GT+). The treatment means were T+, 9·6 : GT+, 10·2 and T−, 21·0 : GT−, 19·0. The daily examinations quickly distorted the zinc strip of GT− so that worms could pass freely beneath the tile. For this reason the treatment failed to show any effect of barriers in preventing entrance, and can only be considered a further replication of 'tile plus dung'. The dung on top of tiles T+ produced smaller numbers of worms than the control of normal dung N (treatment means T+ 9·6 : N, 32·3). The sum of the means from beneath the tile plus dung and the dung itself is, however, 30·6 which is similar to that of the control N, 32·3. Thus, the total attractiveness of the dung was similar but in reducing the number of worms entering the dung on the tile, the tile acted either as a barrier or its under-surface was a more attractive alternative. The ring R prevented access to dung at the soil surface but not from beneath or at a depth of more than 2 cm. Significantly smaller numbers of worms were obtained from dung with this treatment than with the control N (treatment means R, 7·4 : N, 32·3) suggesting that entrance to dung is achieved at the soil surface rather than from beneath.

Table 5. *The percentage of lumbricid species found by soil samples* and dung trials*

	Without raw humus soils		Mixed alluvium soils	
	Soil samples	1954 dung trial 1	Soil samples	1954 dung trials 2-5
Number of specimens	610	1023	1217	2270
PIGMENTED GROUP				
Lumbricus sp.	31·2	65·7	8·4	59·3
Dendrobaena rubida	4·6	27·5	4·6	24·9
D. octaedra	0·2	0·3	0·9	5·7
Bimastus eiseni	–	0·1	–	0·1
UNPIGMENTED GROUP				
Allolobophora caliginosa	25·6	1·5	14·4	0·4
A. chlorotica	11·6	4·4	53·1	8·8
A. terrestris	7·0	0·1	–	0·1
Octolasium cyaneum	18·5	0·1	6·2	0·2
Eisenia rosea	1·3	0·4	12·3	0·4
Eiseniella tetraedra	–	–	0·1	0·1

* The soil sample results included in this table are taken from Svendsen (1957).

Entrance to dung from beneath but not at the surface was prevented by the blocked funnel treatment G which produced a significantly smaller number than the control N (treatment means G, 12·3 : N, 32·3). However, if entrance to dung occurs mainly at the soil surface then the sum of the treatment mean of G with that of R should exceed the treatment mean of the control N; this it fails to do (Σ G and R, 19·7 : N, 32·3). The totals from the pilot experiment of 1953 for these three treatments were R, 60; G, 125 and N, 142 so that here R + G does exceed N. The treatments G in the two years differed in that in 1954 there was an interval of approximately 2·5 cm between the dung and the natural soil surface and the soil beneath the plate had been disturbed in placing the blocked funnel. Thus G of 1954 may be more comparable with T+ (treatment means G, 12·3 : T+, 9·6), the interval of tile or plate between the dung and natural soil surface acting as a barrier to entrance. Alternatively, the environment of these two treatments may have differed from the control N in being less sheltered by surrounding vegetation. There was, however, no difference in the effects of sites or replications on treatments although the amount of vegetation cover varied a great deal. If the dung-seeking Lumbricidae were extremely sensitive to dung odour small reductions in the quantity of dung products would result in lower numbers of attracted worms. This may explain the low numbers of the blocked funnel treatment (G, 1954) where the disturbance of the soil necessitated in sinking the funnel may have reduced the spread of dung products. Such sensitivity would also account for the observed differences where different dung volumes were used.

Although only small numbers of the unpigmented species were found by the trials a high proportion of their members were found to be mature.

	Mature forms	Immature forms	Total
Unpigmented species	153	139	292
Pigmented species	938	2333	3271
Total	1091	2472	3563

$\chi^2 = 72{\cdot}1$; $P = 0{\cdot}001$

Surface activity which might have led to aggregation in dung was investigated when it was found that small numbers of the unpigmented species were surface active at night during wet weather. Here again a high proportion of their members were mature, and it was thought that their activity was associated with their sexual state (Part II). A significantly high proportion of mature to immature specimens and of the unpigmented species *Allolobophora chlorotica* was found beneath the tiles with dung on top T−. Conversely, both proportions were significantly low in dung on top of tiles, T+. The proportion of the unpigmented species *A. chlorotica* was high beneath tiles with dung because to some extent this simulated a soil habitat, and for the opposite reason was low in dung on top of tiles. The reason for the high proportion of mature forms found beneath tiles with dung is obscure. The proportion may have been influenced to some extent by the relatively high numbers of *A. chlorotica* but the effect was also observed in site 6 where this species did not occur.

Significantly high proportions of *Dendrobaena rubida* and low proportions of

Lumbricus rubellus occurred in treatment R, where access to the dung via the surface was prevented. This may have reflected a difference of behaviour between the species suggesting that *Dendrobaena rubida* either moved slightly deeper than *Lumbricus rubellus* or was more liable to climb a barrier. In the latter respect it is interesting to note that this species is recorded as often climbing trees by Cernosvitov & Evans (1947).

PART II. LUMBRICID ACTIVITY RELATED TO TEMPERATURE, DARKNESS AND RAINFALL

Six species, *Lumbricus rubellus, L. castaneus, L. festivus, Dendrobaena rubida, D. octaedra* and *Bimastus eiseni* were found to aggregate in dung as a result of movement at or near the soil surface (Part I). The following section is concerned with the environmental conditions which allowed this activity, and both the records of aggregation in dung (Part I) and direct observation were used to measure it. Observation of lumbricid activity is hampered by the nature of their habitat. On occasion, however, the above species and *Lumbricus terrestris* were active at the soil surface when direct observations were made.

Table 6. *Lumbricidae from a collection made at the soil surface at night*

	Free on surface		'Tail' retained in burrow	
PIGMENTED SPECIES	No.	%	No.	%
Lumbricus terrestris	4	3·1	127	93·4
L. rubellus	46	35·9	5	3·7
L. castaneus	21	16·4	–	–
L. festivus	16	12·5	1	0·7
Dendrobaena rubida	16	12·5	–	–
Total pigmented species	103	80·5	133	97·8
UNPIGMENTED SPECIES				
Allolobophora terrestris f. *longa*	3	2·3	3	2·2
A. caliginosa f. *typica*	15	11·7	–	–
Octolasium cyaneum	4	3·1	–	–
Eisenia rosea mut. *macedonica*	3	2·3	–	–
Total unpigmented species	25	19·5	3	2.2
Total	128		136	

(*a*) *Direct observation on surface activity*

At Moor House no appreciable lumbricid activity was observed on the soil surface during daylight, and none at night during frosty or dry conditions. During the hours of darkness, however, when the soil surface was wet from rain (heavy dews were not effective), two distinct types of lumbricid activity were observed. Thus while some worms retained their 'tails' (several hind segments) within their burrows, others moved over the surface entirely free from their burrows. Worms were collected separately on several nights and their numbers and species are given in Table 6.

Hogben & Kirk (1944) writing of *Lumbricus terrestris*, state: 'the earthworm is not equipped to emerge from its burrows except when the surface of the soil is exceptionally cool and moist'. Dreidax (1931) found only one species, *Lumbricus terrestris* active at night, and similarly this species was alone in a collection made at night in the U.S.A. and examined by Evans (1948). The latter author, however, stated that three species of the 'tail in burrow' type were active at night at Harpenden, England, naming them as *Lumbricus terrestris*, *Allolobophora terrestris* f. *longa* and *A. nocturna* Evans (Evans 1947). Darwin (1881) after Morren (1829), refers to the habit of 'the earthworm' in retaining its 'tail' in its burrow when surface active at night, and in pot experiments found worms very sensitive to vibration, withdrawing immediately when so disturbed. Again by pot experiments Darwin found that worms reacted only slowly to stimulation by light, but would not emerge at all from pots kept artificially illuminated. Observations on the 'tail in burrow' type at Moor House agreed with Darwin's findings. Neither Darwin nor the present author recorded critical illuminations or measured the light intensities used.

Table 7. *The proportions of pigmented and unpigmented Lumbricidae found by night collection and soil samples*

	Pigmented species	Unpigmented species	Total
Soil samples	168	221	389
Free on the surface at night	103	25	128
Total	271	246	517

$\chi^2 = 53{\cdot}02$; $P = 0{\cdot}001$

Table 8. *The proportions of mature and immature specimens of pigmented and unpigmented species found in a collection made at night*

	Pigmented species	Unpigmented species	Total
Mature forms	49	23	72
Immature forms	54	2	56
Total	103	25	128

$\chi^2 = 16{\cdot}35$; $P = 0{\cdot}001$

Of the species given in Table 6 it seems that *Lumbricus terrestris* is practically unique in retaining its 'tail' in its burrow. Because of the extreme sensitivity to vibration of the 'tail in burrow' type capture must be rapid and diagnosis of the behaviour visual and immediate. With the exception of *Allolobophora terrestris* this necessity for rapid diagnosis is thought to be a source of error sufficient to account for the occasional records of other species found with their 'tails in burrows'. The numbers of *A. terrestris* in both types of night collection were equally small.

Of the Lumbricidae found free on the surface several species are concerned which, at least at the time of the collection, rarely included *Lumbricus terrestris*.

Conclusions based on the numbers of these species are limited since the numbers living in the area from which they were obtained are not accurately known. However, 1 sq. m of the area to a depth of 20 cm was dug and the worms removed by hand sorting (Svendsen 1957). The totals of the pigmented and unpigmented group of species in the two collections are compared in Table 7 from which it is clear that a high proportion of Lumbricidae moving over the surface at night belonged to the pigmented group of species. The proportion of mature to immature specimens of the pigmented and unpigmented groups of the night collection 'free on the surface' are compared in Table 8, which shows a significantly high proportion of mature specimens in the unpigmented group.

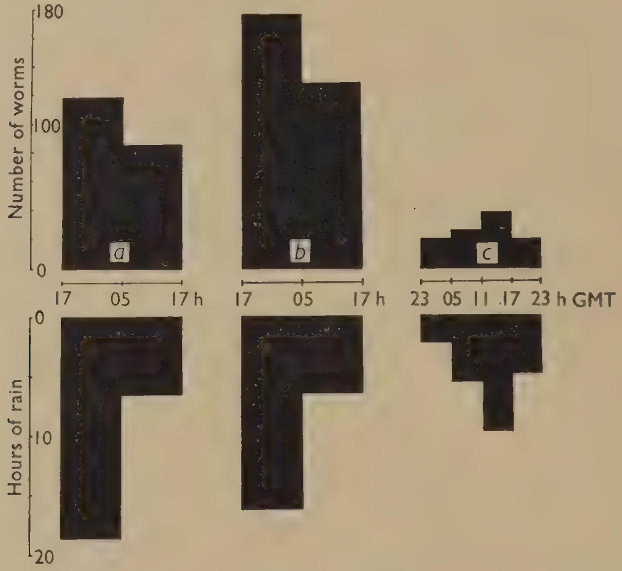

Fig. 1. Numbers of worms collected from prepared dung, together with hours of rain. *a*, the sum of six days' collection at 0500 and 1700 h G.M.T., 15-21 September 1954; *b*, the sum of six days' collection at 0500 and 1700 h G.M.T., 15-21 September 1956 (differs from (*a*) in that collections started 12 h later); *c*, the sum of five days' collection at 0500, 1100, 1700 and 2300 h G.M.T., 8-12 June 1954.

The analysis of Tables 2 and 3 (Part I) suggested that surface movements were relatively uncommon in the unpigmented group of species, and Table 8 suggests that when they did occur they were associated with the sexual condition of the worms.

(*b*) *Activity measured by records of aggregation in dung*

The result of movement during hours of darkness relative to daylight was measured by examining sites of prepared dung at regular intervals. During 8-12 June 1954 worms were collected from one site at 0500, 1100, 1700 and 2300 h G.M.T. and during 15-21 September from two sites at 0500 and 1700 h G.M.T. The effect of rain was important and the number of hours of rain are included in the results shown in Fig. 1. The influence of rain, irrespective of daylight and darkness, was assessed by collecting worms at twenty-four hour intervals. Fig. 2 shows the numbers obtained on one site for the 15 days from 2-16 June 1954 along with the rainfall recorded at the meteorological station near the experimental site by a daily continuous rain recorder. The number of hours rain for the periods involved are given as more relevant than the amount in millimetres. Differences between totals obtained from six-hour periods (21 : 25 : 37 : 19, Fig. 1*c*) are not significant, and the dark period, 2300-0500 h, did not produce the most worms. On the other hand, the numbers found from twelve-hour periods (Fig. 1*a* and *b*) are significantly different and greater for the dark period 1700-0600 h. This apparent contradiction is explained by the association of activity with the state of the ground as measured by the extent of rainfall. Thus, the numbers found from twenty-four hour periods (Fig. 2) are significantly different from each other and closely correlated with number of hours of rain ($r = +0{\cdot}9033$, $z = 1{\cdot}49$, $s = 0{\cdot}289$) and Fig. 1 shows a similar association. There was, therefore, increased activity during rain which was more important than that resulting from the effects of darkness.

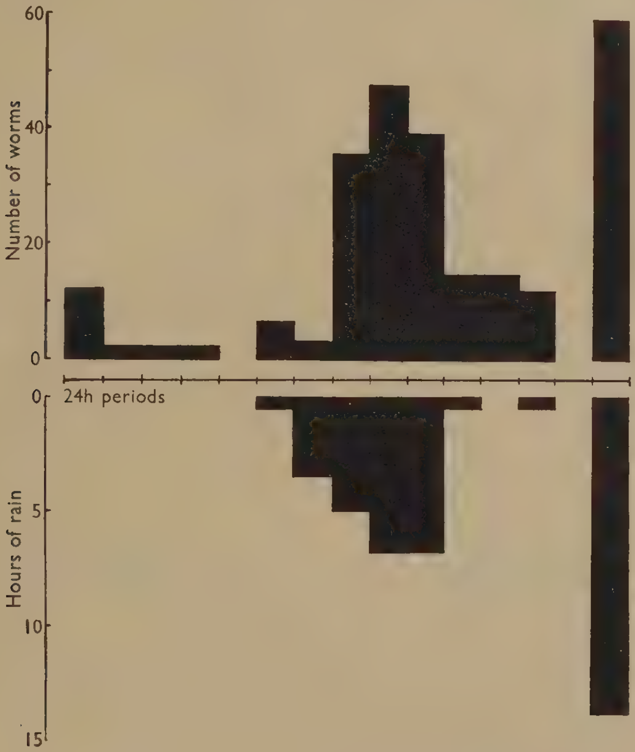

Fig. 2. Aggregation during wet and dry periods, 2-16 June 1954.

(c) *Activity related to temperature*

It was not found possible to obtain satisfactory records of lumbricid movement over a given area in a given time by direct observation. Neither observation nor collection from small marked areas for given periods produced sufficient numbers to warrant statistical treatment. The lowest temperature at which activity was recorded when other conditions were suitable was 3·5° C (grass minimum reading).

The broad effects of temperature may be assessed by seasonal activity shown from records obtained throughout periods of a year or more. For this purpose an area 5 × 10 m of *Calluna* dominant moor was cleared of dung and sampled by fifty 20 cm³ soil cores. Pieces of dung of approximately 300 ml each were deposited at the intersections of a 1 m grid on the area in September 1952. The sixty-six pieces involved were examined and their contained worms collected at irregular intervals during the next two years. The dung was replaced when pieces showed signs of wear. In the initial search of the area eight pieces of dung were found of which four contained eight *Dendrobaena octaedra*. From the fifty soil cores one immature specimen and oötheca of *D. octaedra* were obtained.

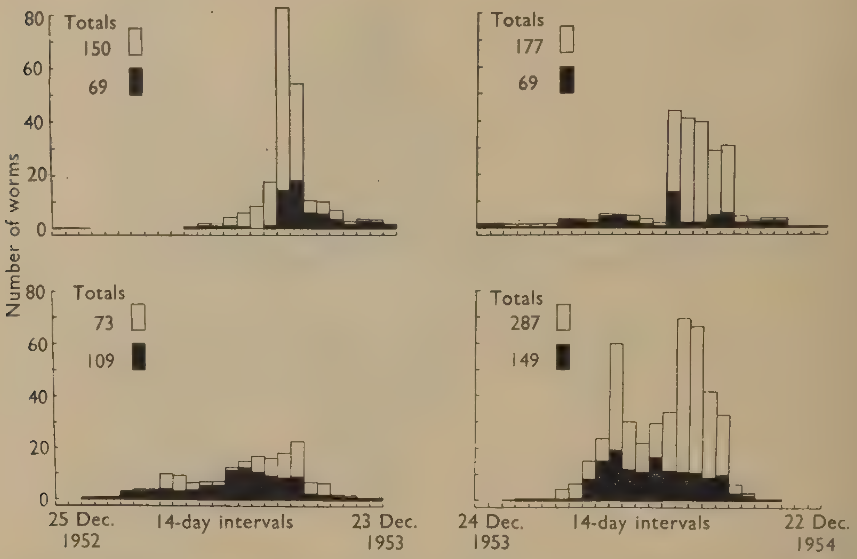

Fig. 3. Worms collected from laid dung calculated as fourteen-day totals throughout the year: above, *Bimastus eiseni*; below, *Dendrobaena octaedra*; ☐, immature; ■, mature.

Two species, *D. octaedra* and *Bimastus eiseni* were found by the examination of the laid dung; their numbers divided into mature and immature forms are shown in Fig. 3. To overcome the effects of the irregular timing of the examinations the totals shown have been calculated as for fourteen-day periods throughout the year. As with direct observation it was not found possible to separate detailed temperature effects from other factors such as rainfall. The summer maxima and winter minima illustrated in Fig. 3 are, however, thought to reflect broad temperature effects.

DISCUSSION

It appears from the paradoxical results of Fig. 1 that species of Lumbricidae found free on the surface at night may be equally active during daylight but then remain concealed within the surface mat of vegetation. Hess (1924) working with *Lumbricus terrestris* stated that this species was light sensitive, reacting negatively to all but the weakest illumination. He also showed (1925) that the sub-epidermal pigment layer of *L. terrestris* acted as a shield to the photo-receptors, so that their stimulation was through 'pin-point windows' formed by nerve endings. Although no comparative work on the light sensitivity of Lumbricidae is known it could be assumed that Hess's conclusions applied equally to all pigmented species, and that they therefore differ fundamentally from the unpigmented group. Thus the pigmented Lumbricidae may be supposed to have a mechanism for controlling the extent of their exposure during surface movements necessary to their nomadic habits, which the unpigmented group lack. *L. terrestris* differs from the other pigmented species in not being nomadic, and darkness may be an essential factor in the feeding period of this species.

The Lumbricidae must necessarily achieve a balance between the dangers of desiccation and endosmosis. They appear to possess little apparatus for water conservation (Stephenson 1930, Grant 1955) and avoid desiccation by the nature of their habitat. Endosmosis is prevented by their ability to pump out excess water (Stephenson 1945, Ramsay 1949, Roots 1955) which is to some extent improved by increased temperature (Stephenson 1930) and differs between species (Roots 1955). Heimburger (1924) and Grant (1955) have shown a positive reaction by a number of species to high relative humidities, and Grant also demonstrated differences between species in their liability to vital desiccation. Thus from the physiological evidence wet conditions would seem necessary to allow surface movements which could be perceived, while, at least for the periods involved, there would be little danger from endosmosis. Roots (1956) showed differences between species in their ability and willingness to withstand total immersion, but considered all species exhibited, some avoiding reaction. This negative response to water she suggested would account for the well-known phenomenon of large numbers of worms found dead and dying after heavy night rain. This did not occur in the author's experience at Moor House, but was seen elsewhere when the deaths occurred on such artificial backgrounds as paths or roads. The presence of worms under these conditions is thought to have followed from the normal nomadic habits described, while their apparent helplessness and later death is attributed to their inability to burrow into paths and roads.

Wolf (1938) found 28 to 30° C lethal to *Lumbricus terrestris* while Rogers & Lewis (1914*a*) found the body temperature of *L. agricola* (now regarded as a synonym of *L. terrestris*) followed that of the environment (immersion in water) closely and rapidly. These authors (1914*b*) considered that the activity (contraction of the dorsal blood vessel) of this species was increased by an increasing temperature within the range 9·5 to 24·6° C. Kim (1930) came to similar conclusions in his work with a species of Megascolecidae. The extent of toleration to low temperature is not known but −1° C is not likely to prove lethal (Allee *et al.* 1949). A soil surface maximum of 25° C was unusually high at Moor House and in any case resulted from conditions which Lumbricidae would not tolerate, direct insolation. Thus there was no reason to suppose that temperatures ever exceeded lumbricid requirements, and judged by the experimental evidence quoted, some reason to believe they rarely reached tolerable maxima. The figure of 3·5° C quoted as the lowest recorded temperature at which activity was observed cannot be taken as more than suggestive. Similarly the seasonal figures given in Fig. 3 do no more than indicate that low winter temperatures restrict activity. It is felt that under field conditions, it is unlikely that more detailed records would prove more meaningful.

ACKNOWLEDGMENTS

I am deeply indebted to Professor J. B. Cragg for his advice throughout this study and to Dr E. S. Page for his help with the statistical treatment of results. The work was financed by a grant to the Durham Colleges from the Nature Conservancy to whom I am also grateful for the facilities offered at Moor House.

SUMMARY

PART I

1. Of the twelve species present, only the six pigmented species, *Lumbricus rubellus* Hoffmeister, *L. castaneus* (Savigny), *L. festivus* (Savigny), *Dendrobaena octaedra* (Savigny), *D. rubida* (Savigny) and *Bimastus eiseni* (Levinsen), clearly aggregated in dung.

2. Increased dung volume (150-600 ml) attracted increased numbers of worms (17·8-57·7). A response to dung products alone was demonstrated.

3. From experiments in which certain types of access to dung were prevented it is possible to state that lumbricid movement into dung generally took place on or near the soil surface.

4. The small numbers of unpigmented species obtained from the dung contained a high proportion of mature forms suggesting that surface movements in these species were associated with their sexual activity.

PART II

5. Only *Lumbricus terrestris* retained its ‘tail’ within its burrow; other species moved entirely free of a burrow system. Of these only a small proportion of unpigmented species were found and these were nearly all sexually mature. The conditions necessary to these activities were found to be darkness, rain and temperatures above freezing.

6. Aggregation in dung was largely restricted to pigmented species. It occurred equally well in daylight or darkness and was markedly increased by rainfall and decreased by dry conditions. Movement in daylight could not be seen and is thought to have been achieved within the surface litter in response to a negative reaction to light peculiar to pigmented species.

7. The effect of temperature was not shown in detail but seasonal records indicated most activity in summer and least in winter.

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THE WINTER FEEDING OF THE OYSTERCATCHER (*HAEMATOPUS OSTRALEGUS*) ON THE EDIBLE COCKLE (*CARDIUM EDULE*)

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(With Plates 8-10 and 7 Figures in the Text)

The presence of large winter flocks of oystercatchers feeding on commercial cockle beds has led to their acceptance, especially by local fishermen, as important predators. Lambert (1951), speaking of the Dutch shellfish industry cites oystercatchers as 'ennemis No. 1 des mytiliculteurs à plat'. The aim of the investigation described below was to study the feeding of the oystercatcher on British commercial cockle beds and to assess the predation. J. A. Gibb (Lack 1954, p. 133) in his study of the feeding of the rock-pipit on a Cornish shore, gives figures for food intake which suggest that birds may be important predators on littoral populations, though the subject has received little attention from marine ecologists. Lack (1954) reviews the literature on the daily food intake of birds in the wild and comments on the paucity of information. In general reliable estimates are difficult to obtain. In the present investigation, with large numbers of birds feeding on the open shore on a plentiful, easily visible food, conditions for observation were very favourable. Laboratory studies of the food requirements of birds are numerous, but their relation to needs in the field, with very different temperature and activity conditions, is uncertain. Dewar, in a series of papers (1908, 1910, 1913, 1915) has investigated the food and feeding habits of oystercatchers in the region of the Firth of Forth. Very little reference was made to the amount of food taken, but the behavioural studies make an interesting comparison with the results given below.

In the present study two areas were chosen for investigation, where the numbers of birds were high in relation to the area of shellfish exploitation, and where the effect of predation was believed to be serious. These areas were the northern end of Morecambe Bay, on the west coast of Lancashire, and Brancaster Harbour, on the north coast of Norfolk. Much more information is available for the former area, but the investigation at Brancaster showed important variations in feeding behaviour, and the comparison is informative. They are treated separately below.

I. MORECAMBE BAY

The location of the cockle bed of Cartmel Wharf is shown in Fig. 1. Cartmel Wharf is some eight miles long and three to four miles wide, bounded on the west by the River Leven, on the east by the Kent Channel, and to the south by the Irish Sea. It is an area of flat sand-banks which dry out to a hard surface at low tide,

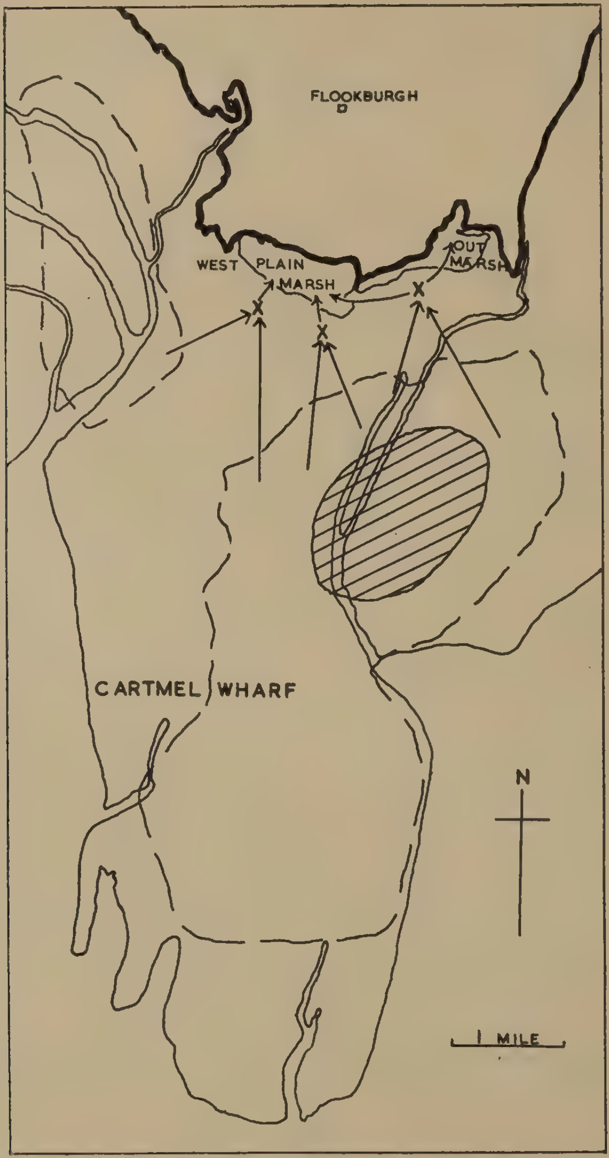

FLOOKBURGH
WEST PLAIN MARSH
OUT MARSH
CARTMEL WHARF
N
1 MILE

Fig. 1. Cartmel Wharf. The thick line marks the shoreline and the thinner line low water of ordinary tides. The area containing cockles in December 1954 is contained by broken lines, and the hatched area is that of the detailed bird observation and cockle population samples. The Xs mark the site of the intermediate sand-flocks and the arrows the movements of the birds with the rising tide.

intersected by drainage gutters. The cockle beds shown on the map extend down the banks for approximately five miles from the tidal level reached after 2-2½ h ebb. The beds begin at a distance of from ¾ to 1½ miles from the coastal marshes.

METHODS

Four visits were made to the area, dating from January 1954 to April 1955. For the earlier part of the winter 1953-54 the observations of the local fishery officer are available, which in no way differ from personal observations made at comparable times in the following winter, and allow with reasonable certainty an extension of the observations to this former period. In all, over 30 days were spent on the cockle beds on which observations were continued throughout the tidal cycle. The period of daylight was covered each day and several visits were made to the beds at low tide periods in the hours of darkness.

The estimation of the predation on the cockle population can be approached in two ways. One can utilize either observed feeding rates of the birds with a knowledge of the numbers present, or the rate of removal of the food population as obtained by visual signs of predation in sample areas. Both these approaches necessitate a knowledge of the size distribution of the food population. In the present study both these methods have their restrictions. In the former the variations in feeding rate, the difficulty of assessing total bird numbers, and the possible effect of an observer are outstanding, and in the latter the uneven distribution of birds and cockles, both temporally in any one area and spatially at any one time, would necessitate an unwieldy sampling programme, though the use of such a method is favoured by the physical conditions, as is seen below. Both methods were utilized in so far as they proved possible and a comparison shows close agreement.

BEHAVIOUR OF BIRDS

(a) *General*

Large flocks of oystercatchers are present in the area only in the winter months. During the two winters studied they were present from the beginning of October to the beginning of March. The summer population is small, comprising the few breeding birds and small flocks of non-breeding juveniles. The source of the birds, that is their breeding area, is of interest in view of their large numbers. Winter recoveries of birds ringed in Britain as juveniles show a general south and west migration but no tendency to concentrate on the west coast of Lancashire. In any analysis of returns of ringed birds one must recognize the bias imparted to the data by the patchy distribution of ringers and collectors. An important source may thus be little represented in ringing returns; this is believed to be the case here.

No accurate estimate of the oystercatcher population of the British Isles is available, but the numbers present in Morecambe Bay in the winters of the study must represent a substantial percentage of this figure. Despite this the number of British-ringed osytercatchers recovered in this area in winter is very low—seven out of a total of eighty-seven such recoveries between August and April. Six of these were local birds from Cumberland and the other originated in Scotland. Foreign-ringed breeding birds have been found in Britain in winter, and three such birds from a total for the country of twenty-three were recovered in Morecambe Bay, two originating from south Iceland and the other from the Faeroes. In Fig. 2 the movements of these birds are shown, together with the details of other winter recoveries on the coasts of Lancashire and Cheshire, of birds from sources over 50 miles distant. It can be seen that these include three more birds from outside the British Isles.

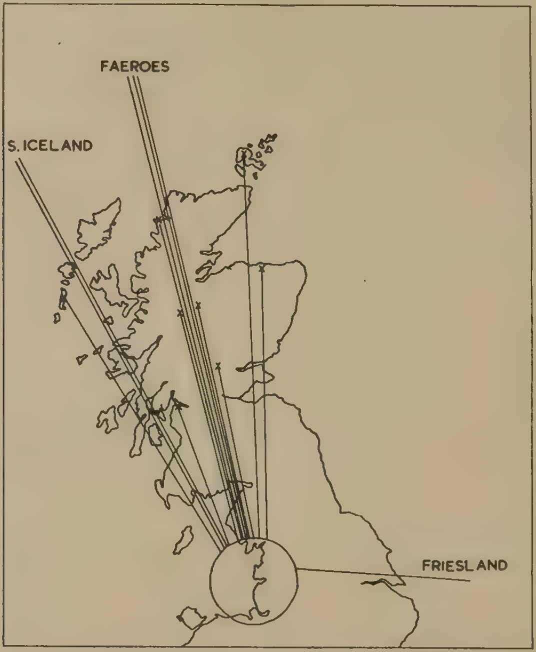


Fig. 2. Winter recoveries of ringed oystercatchers on the west coast. All known recoveries between August and April of birds ringed more than fifty miles from the point of recovery in the circle covering the coasts of Lancashire and Cheshire are shown. The sites of ringing are marked X.

Williamson (1948) notes the very large numbers of oystercatchers which breed in the Faeroes, very few wintering; they depart in late August and return in late March. In Iceland numbers of oystercatchers breed, while some winter there in the south. The ringing returns, coupled with the large exodus in the winter and the coincidence of the dates, suggest that the Morecambe Bay flock contains many birds from these northerly breeding areas.

(*b*) *Daily routine*

The behaviour of the birds shows a regular tidal cycle. Low tide periods are spent feeding on the beds and those of high water on the salt marshes. During the flood the birds retreat before the advancing tide until they are concentrated at the uppermost limits of the cockle beds. When driven from there they fly up to the sands below the salt marshes, where they form 'intermediate sand-flocks', before moving up to the marshes when the tide reaches them. The period of high tide is spent in resting or preening, a time of general inactivity. As the tide ebbs the birds may or may not move down on to the upper sands before flying to the upper limit of the cockle beds when these are uncovered. The birds spread out over the cockle beds, as the tide falls to complete the cycle. This cycle of behaviour is continuous throughout periods of day and night. The fact that the birds fly to and from the beds in the dark is shown by the now discontinued, but formerly widespread, practice of netting them as they returned on an early morning high tide. Observations made at night on the beds confirm that the birds are present and feeding.

Dewar (1915) in his studies of the winter feeding of the oystercatcher on the mussel in the Firth of Forth notes the tidal rhythm and states that 'search for food continues after dark and is evidently carried on much as in daylight', on the grounds of night-time accumulation of faeces. Dewar claims that darkness limits the range of the birds, the more distant feeding grounds only being visited on moonlit nights. No evidence of any such limitation is available from the present study.

The tidal cycle of behaviour is not continued in the summer in inland breeding areas of the oystercatcher (Dewar 1915), but something more than a retreat and advance along the tide line is involved in the behaviour now described, as is shown by the formation of the intermediate sand-flocks some two hours before the tide reaches this temporary resting place, and the lag in following the ebbing tide until the cockle beds are uncovered. Dewar (1915) also describes a fortnightly rhythm of behaviour correlated with the alternation between spring and neap tides. This was shown by an anticipation of the increased height of the spring tides in the settlement on the 'refuge' or high-water roosting place. In the present study no such rhythm was observed, the birds being loath to move higher than necessary on the salt marsh and remaining on the lower regions until lifted off their feet by the incoming water.

The behaviour of the birds in forming the high-water flocks in Morecambe Bay was very regular. Three intermediate sand-flocks of approximately equal size were formed, two on the sands off West Plain Marsh and one off Out Marsh to the east of the promontory formed by the sea wall between the two marshes (Fig. 1). The first two later move up on to West Plain Marsh and join, but the latter splits into approximate halves; one half flies up in small flocks on to Out Marsh, while the other, when driven off the intermediate position by the sea, flies in a long stream round the point to join the West Plain Marsh flock. This behaviour was so constant that it was utilized for the estimation of flock numbers.

Dewar (1915) states that among the winter flocks in the Firth of Forth each has its own feeding territory which it rarely leaves. In that area, where regions of shore unsuitable for feeding occurred between the feeding grounds, this was easily seen. An instance is quoted where flocks sharing the same high-tide roost fed on different grounds. In the present work the stereotyped flocking behaviour suggests the possibility of similar behaviour. The only evidence of a direct nature comes from the movements of an oystercatcher present on the beds in the winter of 1953-54, which had the usual black parts coloured buff. This bird was always seen in the Out Marsh high-tide flock, and when observed on the beds was always feeding in the same area.

(c) *Feeding behaviour*

Feeding behaviour was closely observed during all the visits to the area. The conclusions stated below are based on observations of the opening of some thousands of cockles. The cockle population was dominated, throughout the period of the survey, by the 1951 year-class. In 1953-54 this had attained a length of 20-30 mm, and in 1954-55 25-35 mm (Fig. 3). All the following observations apply to cockles of this size. Smaller cockles were very occasionally seen to be eaten but no detailed observations of feeding on them were made. The oystercatcher swallows only the body of the cockle, after the removal of this from the shell. Hardy (1954) reports 'a wad of cockle shell fragments' from the gut of a bird, but Dewar (1913) states 'the birds [oystercatchers] refuse those portions of the flesh which have got mixed with the fragments of shell driven into them'. In the present investigation shell fragments were never recovered from the guts of birds examined.

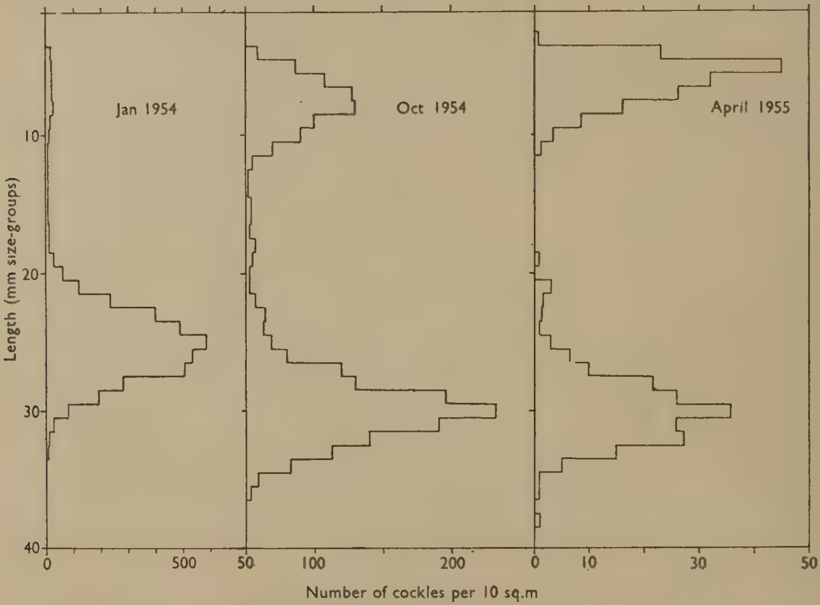


Fig. 3. The size distributions of the cockle population samples in the three surveys on Cartmel Wharf. The numbers refer to 10 sq. m for each millimetre size-group. The differing horizontal scales should be noted.

When feeding on the cockle beds during low tide periods the birds are not uniformly distributed, but are found only on areas which contain cockles, and in these are more dense on those areas where the conditions favour a high feeding rate. On the falling tide this is in the shallow water and the birds follow the retreating shallow region. At low tide any slight dip in the surface which facilitates feeding is exploited. The relation to cockle density was best seen in the late winter of 1954-55, when large cockles were relatively few and patchy in their distribution. Local concentrations were marked by flocks of birds, the intervening relatively bare sand being thinly populated. Even on the relatively featureless sand-banks there is a considerable variety of physical conditions, ranging from shallow gutters, with an inch or two of water, to firm, dry sand on the tops of the banks. The bank tops show all the intermediate stages during the ebb of the tide. The feeding behaviour and the associated phenomena vary with the physical conditions of the substratum and are best considered in that context.

When feeding on cockles which are covered by water, the oystercatcher wades slowly forward, head down, with the body parallel to the water and the beak vertical. Probing of the sand may occur but location appears to be by sight in the majority of cases. When a cockle is found a series of vigorous vertical jabs is made, followed by horizontal levering movements of the head and bill. On uncovered sand the attitude of the bird in seeking cockles is the same but location appears to be almost wholly by touch. In soft sand a series of vertical probes is made without removing the bill from the sand while the bird moves slowly forward. This grades into spaced probes in firm sand. When located, a cockle is levered out by lateral movements of the head with the bill inserted beneath it, picked up between the mandibles and carried some distance before an attempt to open it is made. This carrying of cockles is remarkably constant in its occurrence even on a uniform terrain, the distance moved varying from a few inches to several feet. The opening is effected by a series of vigorous pushes or a tattoo of hard blows delivered with the point of the bill, the choice of method appearing to depend on the size of the cockle. In 1953-54 no hammering was seen, the thrusting being used exclusively. It was in 1954-55 that hammering was first observed, when the cockles were larger, as noted above. The bird is capable of exerting a considerable force by levering from its toes and often leaves a circle of deep toe prints round an opened cockle. The vigorous thrusts from the neck push the cockle into the sand and the hammering can be heard at a range of many yards. If an attempt at opening proves unsuccessful the cockle is once more picked up, carried some feet and the process repeated.

The water content of the sand, and therefore its resistance to pressure, appears to be important in opening. In areas of soft, wet sand, concentrations of open shells may be seen on the slight rises. These result from the suitability of such firmer areas for the opening of cockles and the random wandering of the birds in repeated attempts at opening. Chapman (1949) has shown than an increase in sand height by a few centimetres with the resultant loss of water by drainage increases the resistance to penetration, as measured by a penetrometer and the burrowing rate of *Arenicola*. It is suggested that this difference is of major importance to the oystercatcher in the opening of cockles. Associated with the various techniques of opening are differences in damage to the shell and in the rate of feeding. Damage to the shell varies from none at all, when opened under water, to considerable chipping of the valve margins at the point of entry of the bill, or even complete fracture of one valve in the smaller cockles from the banks. The availability of cockles is reflected in the rate of finding and opening, this being greatest in the gutters and least on the high banks.

There is a suggestion that the size of the cockles opened by the birds varies with the force required to open them. This is related to the size and degree of openness of the cockle and to the physical condition of the substratum. Fig. 4 shows a difference in the relation of the opened cockles to the cockle population in January and October, the January sample being smaller relative to the population than that in October. Although the areas from which the opened cockle samples were taken were physically similar, *i.e.* the gently sloping edge of a bank, there is an important difference between them. In the area sampled in January; drainage after uncovering was slight, and concentrations of open shells on slight rises, where the sand resistance presumably became sufficient to allow opening, occurred. In this area birds were occasionally seen to desert cockles after unsuccessful attempts at opening, though this was not seen on covered cockles. It is suggested that this desertion was because the sand resistance was insufficient to support the increased pressure necessary to open the larger cockles when closed, and that this resulted in a bias in favour of the smaller cockles. Cockles of all sizes can be opened when covered and gaping slightly to allow the siphons to protrude. As the tide leaves

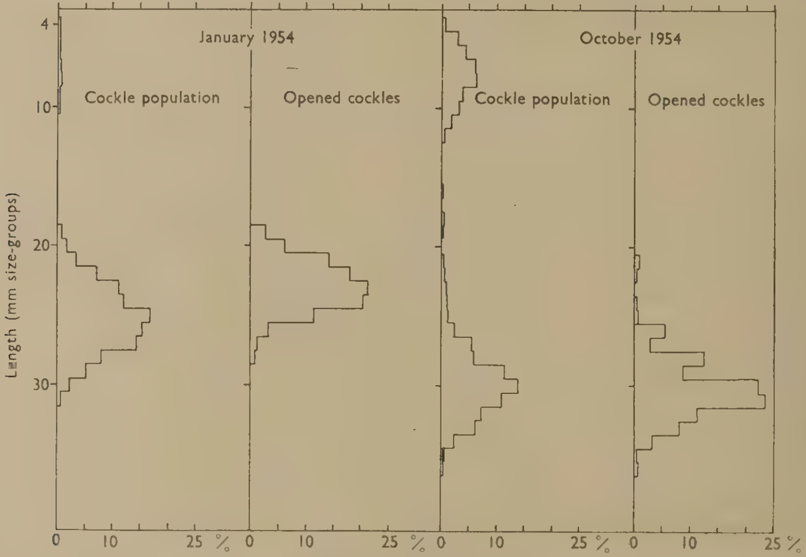


Fig. 4. The size distributions of the shells opened by oystercatchers compared with the cockle population samples, all being plotted in millimetre size-groups as percentages of the sample.

them and they close, the bias occurs until drainage is sufficient to allow the larger ones to be opened. The observations at Brancaster (see p. 464) suggest that a comparable bias may also occur with extreme drainage.

The precise method of gaining entry to the cockle is very difficult to make out by direct observation. Even at close range and with a powerful telescope, the anatomy of the cockle cannot readily be seen owing to the adhering sand. In the following attempt at an analysis of the evidence recourse is made to direct observation, the analysis of ciné films of feeding birds, damage to opened shells, shell anatomy and observations on the feeding of the oystercatcher on other lamellibranch species where the conditions are more favourable to observation.

When covered by water, the cockle is probably tackled when open and feeding, the siphons at the surface providing the evidence of its presence. The first vigorous probes penetrate the parted valves and so no trace of the bill's passage is left on the shells. In the winter of 1954-55 the majority of the cockles were of a length of 25-35 mm and the birds fed almost exclusively on this size range (Fig. 4). The technique employed was a mixture of thrusting and hammering, the latter predominating. Although the shells of cockles on which birds were observed feeding could not be seen clearly, it was determined that attack was restricted to one region of the shell, the bird frequently altering the angle of attack and following this region as the cockle rotated under the pressure of the bill. The bill, having been forced between the shells and these separated by lateral levering of the head, the body of the cockle is removed and swallowed. This is done in two or three mouthfuls, the shell being cleaned except for shreds of the mantle margin and the adductor muscles.

In uncovered sand a cockle is closed, or very nearly so. That no damage is done to the cockle in its removal from the sand has been shown by chasing birds away from newly dug cockles. The closed valves of the cockle fit well, the serrations of the shell edges interlocking and meeting very closely, except for a short distance posterior to the external ligament, where a gap persists at the site of extrusion of the siphons (Fig. 5*a*). Along this posterior border the angle between the valves is more obtuse than in other regions of the shell, the two margins offering less support to one another where they meet. The damage to opened shells varies from the abrasion of an area corresponding to the cross section of the bill, to the chipping of small pieces from the shell edge (Fig. 5*b*, *c*, *d*). In a sample of 1515 opened shells from Morecambe Bay in the winter of 1954-55, 1478 of the shells showed this damage to be confined to the site of siphon extrusion, the persistent gape. Of the others, eleven showed no damage, thirteen showed a fracture of one valve, three had damage to both anterior and posterior margins, and ten also showed damage to the ventral margins of the valves. After opening, the shell frequently remains half buried in the sand, its position being unaltered by the cleaning out of the meat. This position is constant, with the plane of the valve margins vertical and the antero-posterior axis inclined down anteriorly.

During the 1953-54 winter survey the birds were feeding on cockles 20-30 mm in length (Fig. 4). The observed feeding behaviour differed from that of the winter

1954-55 only in the use of pressure thrusts rather than blows, a quantitative rather than qualitative difference. The sample of opened shells, however, presents a different picture (Fig. 5*e*, *f*). Shells from an area analagous to that providing the sample in the following winter, the gradually sloping edge of a bank, showed a fracture of one valve, the break occurring dorso-ventrally and running from the ventral margin of the shell to the region of the umbo. In the sample of 215 shells, 211 showed the anterior end of the valves to be broken off, the direct opposite of damage in the following winter. However, this is not as anomalous as would first appear. The size of the shell opened is the only obvious difference in the situation in the two years. That this is the important variable is supported by the size range of the shells showing valve fracture in the 1954-55 sample. In some way the change in size of the cockle from one winter to the next accounts for the different result

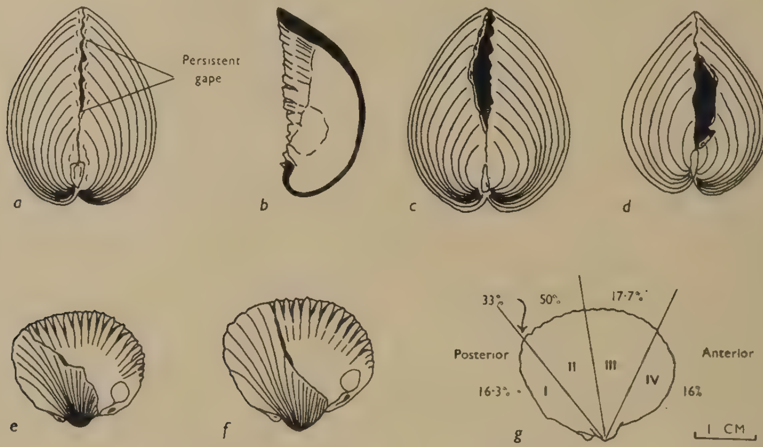


Fig. 5. Damage to opened shells: *a-d*, October 1954; *e-g*, January 1954. *a*, posterior view of intact shell to show the persistent gape. This figure is made up from accurate sketches drawn on the beds. The gape is greater than that of a dried shell in which the valves are pushed together; *b*, section of cockle shell in dorso-ventral median plane; *c*, *d*, typical opened shells in posterior view; *e*, *f*, typical opened shells seen from the right side; *g*, analysis of shell fractures. Figures indicate percentage fractures in quadrants I-IV and at junction I and II.

obtained from very similar treatment by oystercatchers. An explanation is to be found in the structure of the shell of the cockle.

Shell deposition in the cockle occurs mainly at the mantle margins, resulting in a shell which becomes thicker at the margins with increasing size and the resultant decreased rate of linear growth (Fig. 5). At the margin the shell is thinnest under the ribs. Thickening and incorporation of organic material into the shell occur also in the region of the hinge, the posterior adductor muscle and the persistent gape. In the experimental application of pressure to the valve margins of live cockles, fractures very similar to those of the 1953-54 sample were obtained. This was found to be true for over 200 cockles, no matter where on the shell margin, anterior, ventral or posterior, the pressure was applied. Presumably the fractures follow the line of least resistance in the shell, the structure of which, described above, would suggest such a disposition. Dewar (1908) cites experimental evidence that a fracture caused by such pressure starts from the point of application of pressure. This observation was confirmed by the experiments described above. In the light of this the relative distribution of fractures, and therefore successful application of pressure, over the margin of the valve, was determined for the opened shells in the 1953-54 sample. The shell margin was divided into four regions, two anterior and two posterior to the mid-line. The results are shown in Fig. 5*g* and show a high count in the posterior half of the shell. Closer analysis shows that the excess in the posterior ventral quadrant, II, occurs at the junction of this and quadrant I at the ventral end of the persistent gape.

The persistent gape is narrow in cockle shells 20-30 mm in length and would scarcely admit the tip of the oystercatcher's bill, since the chisel-like end is soon rounded off in the young oystercatcher by abrasion. It was fine enough to enter the gape of shells of this size in very few of the many dead oystercatchers examined in this study. The high proportion of fractures in this region is probably due principally to the lack of support of the shells for one another in resisting pressure on account of the gap between them and the less oblique angle they present to one another. The increased thickness of the valve at the dorsal end of the persistent gape compensates to some extent for this inherent weakness.

The following conclusions emerge from the above discussion. Cockles are opened by the random application of pressure by the bill to the valve margins. The result of this varies with the size of the cockle tackled. In cockles up to a size of approximately 30 mm a fracture runs from the point of application of the bill to the dorsal margin of the shell anterior to the umbo. Fractures start from all points on the margin but show a concentration on the anterior end of the persistent gape, where the shell is most vulnerable. In larger shells the increased marginal thickness demands a much greater force to achieve such a fracture and entry is gained by forcing the shells apart, with much less extensive damage, at the persistent gape.

A bias may have occurred in the collection of the 1953-54 sample, as opened shells were collected over a wide area, and to prevent confusion shells with the valves separated may have been discarded. This would have excluded any shells showing a fracture which caused a break in the hinge. The experimental results above, however, suggest that such shells are unlikely to occur. In 1954-55 all shells were collected from defined areas and no such bias could have occurred.

(*d*) *Comparison with accounts of feeding on other shellfish*

Location of cockles in sand is by touch. Dewar (1908) describing the feeding of the oystercatcher on mussels buried in sand reached a similar conclusion. Tapping to gain entry to *Mytilus* has been described by Dewar (1908) when the damage to the shell closely resembled that noted in the present study. Dewar described also the restriction of blows to the margins of the valves. Tomkins (1947) in an account of the feeding of the American oystercatcher, *Haematopus palliatus palliatus*, on the American oyster described pressure thrusts directed at the valve margins. The carrying of bivalves before opening has been noted (Dewar 1908, 1913), and the orientation of food before attack in the case of feeding on *Modiolus* (Dewar 1908). Personal observations of oystercatchers feeding on *Mytilus* in North Wales have shown that orientation of the animal so that the more vulnerable ventral margin is uppermost, and the subsequent direction of the attack to this region, is the normal method of feeding. This observation is at variance with Dewar's accounts of feeding on *Mytilus* but agrees with his remarks with reference to *Modiolus*. Certainly a high degree of orientation of the shell is possible, but it is doubtful whether the oystercatcher orientates large cockles so that the persistent gape is uppermost. In the observations in North Wales on feeding on *Mytilus* a bird frequently stopped its attack to re-orientate the shell but attack was general over the ventral margin of the valves. In the observations on feeding on *Cardium* re-orientation only took place when a shell was moved in between attempts at opening. The undisturbed cockle lies in the sand with the siphons uppermost and this may increase the chance of this region being uppermost when attacked after having been carried. A general restriction of attack to the valve margins is a feature of the oystercatcher's method of feeding on bivalves, and it is suggested that the opening of *Cardium* at the most vulnerable place is the result of random attack along the valve margins, leading to success where this is most easily gained.

It is worthy of note that the majority of the cockle shells examined showed damage to one valve only. Dewar (1913) noted this in the opening of *Mytilus*, *Modiolus* and *Tapes*. In the case of *Mytilus* Dewar describes an uneven pressure of the bill due to its descent at an angle oblique to the medial plane of the mussel causing a rotation of the valves on one another and so an increase in the vulnerability of the raised valve. In the case of the cockle no such rotation would be possible on account of the interlocking shell margins and hinge-line teeth. The inequality of damage to the two valves can only be ascribed, in the absence of further information, to some inequality of pressure. In the experimental application of pressure, precisely corresponding fractures of both valves were produced from pressure applied to the shell margin. Only if one valve alone was subjected to pressure was the single fracture obtained.

In discussing the opening of *Mytilus* through the dorsal border, where damage to one valve is caused by lateral movements of the head, Dewar (1908) notes that the left valve is more often injured than the right owing to the tendency of the oystercatcher to lower its head to this side. In all the opened cockles studied in this survey, where only one valve was injured, there was no suggestion of a comparable phenomenon. In over 2000 shells examined the frequency of damage to right and left valves was in the ratio 1 : 1.

FOOD INTAKE

(*a*) *Method of estimation*

The daily food intake of the birds is based on the observation of individuals for periods of from 10 to 15 min, coupled with periodic counts of the percentage of birds feeding in the flock under observation. These observations were made at all states of the tide when the birds were feeding. It was found desirable to stay in one place on any one day so that bias due to concentration on actively feeding flocks for the percentage feeding counts could be avoided. The majority of the feeding estimates are from one area (see Fig. 1) of which the cockle population was well known and where a dyke draining a hollow surrounded by hard-drying banks provided a relatively isolated area with a small, practically discrete, population of birds. This population was used as the unit for percentage feeding counts. In this way the nearest possible approach was made to the ideal of long-term observation of individual birds, a very difficult task on account of their density and extreme activity. It was found that the rate of feeding varied considerably with the physical conditions prevailing in any area and the density of food. The uniformity of the physical conditions of the feeding ground in the sample area prevented any possible bias due to the selection of birds for timed feeding counts from a population with widely varying feeding rates. That this restriction of observations to any one set of physical conditions is justified is supported by the extreme similarity of the estimated food intake at both Morecambe Bay and Brancaster, and at different times, described below. Many observations in other areas of the beds showed that the behaviour of the birds on the test area was not abnormal. The birds showed little reaction to a human observer, being accustomed to the activities of the cockle fishermen, and as long-distance observation with a telescope was normal the influence of this factor can be ignored.

Estimates of the removal rate of cockles are available from the counting of opened shells in a marked area, in which a known number of birds had been feeding for a known time.

A number of birds were killed during the surveys for gut analysis. The gut contents were preserved as soon as possible after killing. No identifiable remains penetrated further than the gizzard so the following procedure was adopted in preservation. After the opening of the bird the gut was tied off just below the mouth and at the beginning of the duodenum. A 5% solution of formalin was injected into the gizzard and oesophagus and these were removed and stored in bottles of 5% formalin. In the counting of contained cockles the foot was used as the unit, this being the most persistent and easily recognizable part of the body.

(*b*) *Results*

During the time that the birds spend on the beds, feeding is continuous on a flock basis, though individual birds show an alternation of feeding and rest periods. In the following account, the term 'feeding rate' will be used for the rate of taking food during a period of feeding, and the term 'overall food intake' for the average rate of feeding over both feeding and non-feeding periods added together. Detailed estimates of the feeding rate were made on two of the visits to the area, in January 1954 and in October 1954. Observations made on all other visits to the area, although not sufficiently comprehensive for detailed analysis, showed no departure from the results now used.

In January 1954 counts were made on six individual birds at intervals scattered throughout the low tide period for a total time of 91 min (Table 1). The observed feeding rates varied from 32 to 64 cockles/h with an average of 51 cockles/h. During many additional hours of observation of feeding birds this rate was seen to be general, though severe weather conditions made recording impossible. The relatively few detailed counts are therefore considered to be reliable. The percentage feeding counts were made on a total of 530 birds, the counts being made on many small flocks throughout the tidal cycle. The variation in percentage feeding throughout the low tide period was very small. Even when the beds were first uncovered and some flocks showed 100% feeding, other flocks nearby would show a small percentage feeding and these birds would only start feeding when the water level fell. The average percentage feeding figure for all the observations was 42%. So the calculated overall food intake throughout the low tide period was 21 cockles/h/bird.

Table 1. *Observations on feeding rates*

JANUARY 1954: six birds observed.

	Number of cockles eaten	Time for which bird was observed (min)	Feeding rate (cockles/h)
	13	15	52
	15	15	60
	17	16	64
	8	15	32
	10	15	40
	15	15	60
Total	77	91	308

Mean of all observations: 51 cockles/h

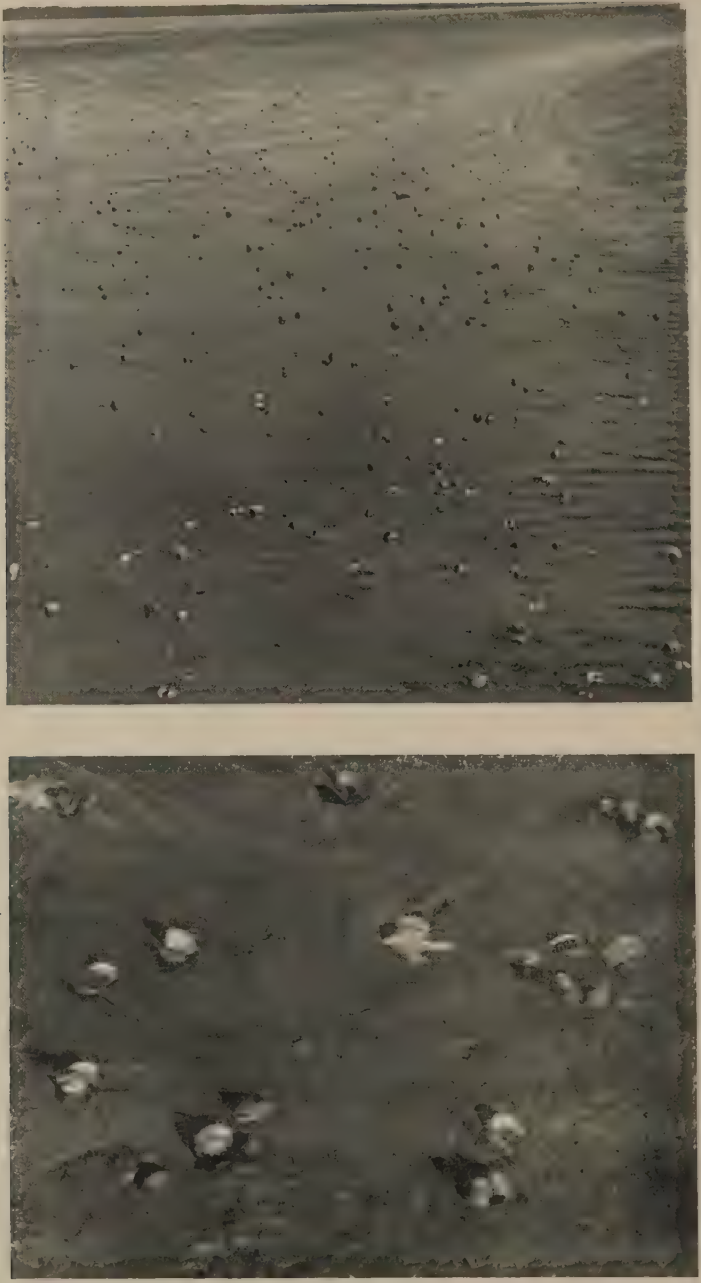
OCTOBER 1954: numbers of cockles eaten in a 10-min period by individual birds; 34 birds observed.

Cockles eaten in 10 min	Number of birds feeding at rate given	Feeding rate (cockles/h)
7	1	42
6	1	36
5	25	30
4	4	24
3	2	18
2	1	12

Mean of all observations: 4·75 cockles/10 min = 28·5/h

In October 1954 the methods employed were similar to those of the earlier visit. Detailed counts were made on thirty-four birds for a total time of 340 min (Table 1). Observed feeding rates varied from 12 to 42 cockles/h, with an average figure of 28·5. In the many hours of observation of feeding birds, it was seen that a rate of about 30 cockles/h was general, though weather conditions frequently prevented detailed observation. Percentage feeding counts were made on a total of 1241 birds and gave an average figure of 50%. The overall food intake thus obtained was 14·25 cockles/h/bird.

During the period of high water the cockle shells opened on the preceding low water become bedded into the surface sand and so a clean surface is presented at



Typical opened cockle shells in area of observation, April 1955. The concentration here is above average. Below: a close-up of part of the upper photograph.

(*Facing p.* 455)

the next low water. Thus Plate 8 shows cockles opened since the high water preceding the photograph. Thus a check could be made on the food intake results, arrived at by the observational method. In October 1954 a large area of sand was staked out on the sloping bank on which many of the feeding rate counts were made. The number of birds feeding in that area was counted at frequent periods for some hours after the beds were uncovered, care being taken to use a telescope for this at a range of several hundred yards so as not to affect the behaviour of the birds. After the area had been uncovered for some hours the birds were driven off and an estimate of the open shells made. Even though the absence of shells from the area at the time of uncovering was highly probable, all the collected shells were examined and only those which retained shreds of mantle and adductor muscle were counted. On the first day the marked area was observed for 2½ h after first being uncovered. The bird population during this time varied from 47 to 69 with an average of 56. Opened shells were collected from twenty-nine random areas, each of 25 sq. yd, and totalled 117, an average of 4 per 25 sq. yd. The area staked out was 15 500 sq. yd approximately, and an estimate of 2480 opened shells in that area is obtained. This gives the average number per bird for the period of 2½ h as 44, an overall intake of 17·6 /h/bird. On the next day a slightly larger area, 18 700 sq. yd, was counted after having been uncovered for 2 h with a bird population ranging from 52 to 67 and averaging 57. All the opened shells in this area were collected and totalled 1515. This gives a figure of 26·6 per bird for the two-hour period and an overall intake rate of 13·3 cockles/h/bird. Owing to the time required for estimation of the numbers of opened shells in any such area, it was not possible to study by this means any other period than the first few hours after exposure. However, the observational methods have shown that variation in feeding rate throughout the low tide period is small. Estimates of the overall food intake for this period of October 1954 are respectively 14·25, 17·6 and 13·3 cockles/h/bird. It will be seen that the agreement between the results obtained by the different methods is close.

When the estimates of food intake are compared for the two winters it is seen that the figure for 1953-54 is 50% higher than that for 1954-55. However, in view of the differing average size of the cockles eaten during these periods a comparison of the volume or weight of the intake was made. In Fig. 6 is shown the relationship between the length of a cockle and the volume of its meat. In obtaining this relationship the volume of the meats of 5-10 cockles of each size-group was measured by water displacement and an average figure calculated. These figures were obtained from Morecombe Bay cockles in February 1955 and may not be strictly relevant to food intake at any other time or place. As, however, the volume intake was not considered till this time, data on cockles at an earlier date are unobtainable. The mean length of the cockles eaten in January 1954 (Fig. 4) was 22·86 mm, and in October 1954 30·29 mm. The respective volume figures for these sizes are 0·96 and 1·82 ml. So applying the food intake figures given above we obtained a food intake volume of 20·16 ml/h for January 1954 and 25·94 ml/h for October 1954. The probable error in the calculation of these figures does not allow a close comparison, but it is perhaps relevant to note that the activities of the birds in the two surveys, as measured by the amount of time spent in feeding (the major activity showing any variation) varied in approximately the same ratio. However, intake rate is probably governed by a much more complex mechanism, such factors as condition of the birds, temperature and the food value of the cockle at different seasons being of importance. There is also the possibility that the restriction of the opened cockle sample in October to the first few hours of feeding, when many of the cockles were covered when attacked, may have resulted in a bias in favour of the larger cockles and a slightly higher estimate of the volume taken.

The value of the analysis of gut contents in the estimation of food intake is very small without a precise knowledge of the rate of digestion. Birds were shot in the winter of 1953-54, both on the beds and on the salt-marsh roosts. Thirteen birds shot on the beds at various times during the low tide period were found to have from twelve to twenty-three cockles in the oesophagus and from thirty-seven to forty-four cockles in the gizzard. Some estimate of the rate of digestion can be obtained, since the guts of twenty-one birds shot on the marshes from 2-4 h after leaving the feeding area contained no identifiable remains. This suggests that the estimated food intake rates are well within the capacity of the birds' digestion. Dewar (1915) states, 'the process of digestion and excretion in the oystercatcher is very rapid', but gives no more detailed information.

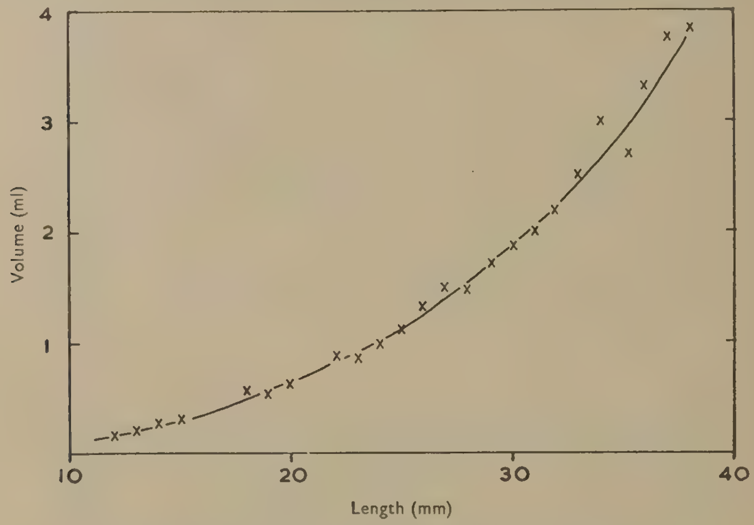


Fig. 6. Relation between length and volume of meat of cockles.

The literature on the feeding of the oystercatcher contains little reference to food intake. Dewar (1913) mentioned a bird which was observed to take mussels of from five-eighths to seven-eighths of an inch in length at a rate of seven or eight a minute for three-quarters of an hour. As he noted, 'thus it must have cleared upwards of four hundred shells in one hour'. In this instance the shells were rarely well cleaned, and with no estimate of the relation of the period of observation to the total daily period spent feeding, this isolated observation cannot easily be compared with the results given above. The rate of feeding varies enormously with the availability of the food. To cite an example, feeding rates of over 200 cockles/h were observed in October 1954 within the small area in which the observations cited above were obtained. These occurred in a very restricted area of shallow water where the action of a drainage channel had caused a dense concentration of cockles.

Although the birds feed in the dark at low tide periods, no method of estimation of the feeding rate at this time could be devised. At dawn the density of opened shells on the beds did not differ greatly from a comparable time during the daylight cycle, as estimated by eye. From the knowledge of the feeding method there appears to be no reason why the food intake should be any less in the dark, except in the case of cockles located by sight which make up a small fraction of the total cockles eaten. Even with a greatly reduced feeding rate at night the balance of time left for feeding, not utilized during the day, could be used to make the overall intake equal.

The effect of weather conditions on the feeding of the oystercatcher is discussed by Dewar (1915) who states: 'In winter the influence of variations in climatic conditions is mainly an indirect one [on the food], for the oystercatcher is extremely hardy, no extremes of temperature or humidity likely to occur in the Forth area seeming to have any harmful effects. Torrential rain inhibits all except compulsory movements until the need of satisfying hunger becomes paramount. Really hard weather increases the food activities . . .' In Morecambe Bay the effect of weather conditions was not marked except in the case of a day of extremely high wind in January 1954, when a westerly gale with gusts of over 90 m.p.h. prevented feeding completely. The heavy rain, hail and wind made flight almost impossible and any attempt at feeding resulted in a loss of balance. In all other conditions of weather, many of which were severe, including a layer of ice $\frac{1}{4}$ in. thick on the beds, feeding was not noticeably affected.

(*c*) *Food*

Many workers have listed the food organisms found in the gut of oystercatchers from many parts of Europe. Although its heavy bill is generally stated to be adapted to deal with bivalve molluscs, the list is surprisingly varied. A notable feature of the food is the annual variation, since in the summer inland breeding areas a wide variety of terrestrial invertebrates is taken. Marine organisms eaten on the coast, although predominantly bivalves, also include all major groups of the littoral fauna. On the area in which the birds were feeding, cockles were the most obvious component of the fauna. The cockle population surveys showed that the other animals present in significant quantities were two bivalves, *Tellina* and *Macoma*, and a small nereid worm. None of these forms was abundant and their densities were generally far below that of cockles. During the observation of individual birds they were occasionally seen to take *Tellina* and *Macoma* from

1-2 cm in length. Swallowing movements were also seen during the typical food-searching behaviour, which probably accompanied feeding on the nereid. In some limited areas *Macoma* was eaten in larger quantities, as measured by the opened shells, but the importance of all these forms in the total diet of the birds in the area was very small. In all the guts examined no other food than *Cardium* was seen. The complete emptiness of the guts of birds on the marsh or returning to the beds showed that no feeding took place there. It will be seen that the size distribution of the eaten cockles follows that of the population fairly closely except that the smaller cockles (below 20 mm) present on the beds in October 1954 are not represented in the opened sample. Dewar (1915) states that oystercatchers feeding on mussels in the Firth of Forth show a preference for animals of 3·5 cm in length. 'Probably mussels ranging closely about this size provide food in due proportion to the amount of labour required to get it.' In the present study no such preference was seen, perhaps a consequence of location by touch rather than by sight in the majority of opened cockles.

NUMBERS OF BIRDS

The author has been unable to find in the literature an account of a satisfactory method of estimating large numbers of birds unless they are related to some fixed object such as the nest in the breeding season, or are semi-sedentary and relatively fearless of man. Eye estimation is very crude and inaccurate unless related to flocks of known size. No method could be conceived of estimating the bird numbers when they were feeding on the beds. The classical method for such estimates, of counting the numbers of birds encountered on transect walks, was precluded by the uniformity of the terrain with its almost complete lack of landmarks, and the reaction of the birds to such an attempt. An observer on the beds produces an area about 100 yd in diameter which is empty of birds. As he advances the birds retreat ahead and close in again behind. The dense high-water flocks were the target of the estimations, attempts being made on three of the visits to the area, in January 1954, October 1954 and February 1955. Direct counting of the birds in the flocks was found to be impossible owing to their large size (Pl. 9), and the counting of sample sections was inaccurate on account of the density and mobility of the birds. Attempts to estimate the numbers by reference to much smaller flocks which could be counted directly were abandoned because of the highly variable results obtained. The method finally found successful in October 1954 and February 1955 was a photographic one developed from a suggestion by M. G. Ridpath and modified to suit the prevailing conditions. This is to be described in more detail elsewhere.

In January 1954, when the unsuccessful methods outlined above were tried, only an eye estimate of the numbers was reached. The Out Marsh flock, consistently throughout the investigation the smaller of the two, was estimated by eye as one-tenth of the total number of birds. The West Plain Marsh flock, at this time $\frac{3}{4}$ mile in length on the tide line and some 50 to 100 yd in depth, was excluded by its

A. A section of one of the three intermediate sand-flocks which later joined to form the West Plain flock, Morecambe Bay.

B. A typical section of the flock resting on the West Plain Marsh.

(*Facing p. 458*)

A typical section of the Out Marsh flock in flight, used for counting. April 1955 (51 birds).

(*Facing p. 459*)

size from any attempts at estimation. Attempts were made to count the Out Marsh flock as the birds flew up to the marsh from the intermediate sand-flock. It was found, however, that the rate of passing of the birds exceeded the counting capacity of two observers after a total of 10 000 - 20 000 birds had been reached. An eye estimate of this flock was made from counts of sections and multiplication from smaller flocks and yielded 20 000 - 40 000 birds. This estimate is probably highly inaccurate, but is the best available. From the estimated relative size of the two flocks this gave a total population of 200 000 - 400 000 birds.

Attempts were made to photograph the Out Marsh flock in the air when driven from the roost, but proved unsuccessful owing to the weather conditions and the technical limitations of the photographic method. However, the experience obtained showed the possibilities of the method and led to the more successful later estimates. In February 1954 the Royal Air Force kindly attempted aerial photography of the roosting flocks but this proved unsuccessful for technical reasons.

In October 1954 both flocks were driven before a stationary camera and consecutive photographs of the flying birds were taken. This method had the disadvantage that some of the disturbed flock always joined the other resting flock during the disturbance, thus precluding an estimate of both flocks on any one day. However, so far as could be seen, the numerical composition of the two flocks was relatively constant from day to day. The counts gave figures of 3224 birds for the Out Marsh flock, with an estimated 700 not photographed, and 20 215 on the West Plain Marsh. As the field of the camera was often too small to contain the whole of a passing flock, this must be a minimum estimate and the total, 25 000, compares well with an eye estimate made at the time of 30 000 birds.

The purposes of a further estimate made in February 1955 were to measure, as far as possible, the variation in numbers occurring during the winter and to ascertain whether the very large concentrations of January 1954, resulting it is believed from a recruitment of birds from other areas in the severe weather, was a yearly occurrence. The flocks, noted to be larger than in October 1954, refused to behave so conveniently when driven, splitting up and flying erratically round the roost. This difference in behaviour was probably due to the combination of the larger numbers of birds, fewer drivers and the lower tides which enabled the birds to use an almost inaccessible roosting place. However, owing to the stereotyped behaviour in the formation of the roosts referred to above, a modification of the photographic method enabled an estimate to be made.

The Out Marsh flock was estimated by a combination of counting and ciné photography as the small flocks flew from the intermediate sand-flock to the roost (Pl. 10). This gave a figure of 6700 birds. With this method there was the additional advantage that no disturbance of the birds on the roosts was necessary, and the complication of birds flying from one flock to another was avoided. The other half of the intermediate sand-flock to the east of the promontory (Fig. 1) was filmed as it passed the point. Counts of the film were made on an animated viewer, consecutive portions of the flock being compared with photographs of flocks of known size from the earlier stills. This method of visual comparison, as used by Hardy (1938) for plankton investigations, gave figures for successive estimates differing by less than 5% with a mean of 5680 birds. So we obtain a figure for the whole eastern intermediate sand-flock of approximately 12 400 birds. As three such flocks of approximately equal size were present this gives a total of 37 200 birds. Confirmation of this figure was available from the ciné film of the West Plain Marsh flock, made up of the two western sand-flocks and half the eastern sand-flock, which gave a figure of 30 000 - 36 000 birds. The total figures obtained are minimum figures as on each marsh only the main flock was estimated. Smaller flocks, often numbering hundreds of birds, were not included.

The consistent ratio of the size of the Out Marsh flock to the West Plain flock of 1 : 6 in the estimates of 1954-55 suggests that the estimate made in 1953-54 of 1 : 10 may have been low and a total of 120 000 - 240 000 would probably have been more accurate for this period. It can be stated with certainty that the number of birds present in the winter of 1953-54 was undoubtedly higher than at any later visit. This high density may have been due to the exceptionally severe weather conditions of that winter, as has been suggested earlier, or may have been connected in some way with the much higher cockle densities prevailing at that time.

COCKLE POPULATION

The cockle population was sampled at Morecambe Bay in January and October 1954, and in April 1955. A series of stations was made, each being located on the bed by compass bearings of landmarks, and of one another. At each station the sand from five squares, each 0·2 sq. m, was dug out and washed through a fine sieve. All the cockles from these sievings were measured to the nearest millimetre below, the greatest length on the antero-posterior axis being recorded. The huge size of the beds coupled with the time and labour involved in the transport of sampling gear precluded any sampling of the whole area, but visual estimates of the rest of the bed showed that the area selected was typical. In the three surveys the area sampled was the same and included that in which the majority of the feeding data was obtained.

In January 1954 fifteen stations were sampled, and a total of 5552 cockles measured. In October 1954 1568 cockles were measured from twelve stations and in April 1955 480 cockles from fourteen stations. The size distributions of the population at the three surveys with the densities per 10 sq. m are shown in Fig. 3. It can be seen that the population was dominated throughout the survey by the larger cockles of the 1951 year-group. It is this size-group (Fig. 4) which formed the food of the oystercatcher and which concerns us here. Settlement of young cockles, in subsequent years, was very slight and not sufficient to replace the adults lost.

In January 1954 cockles between 20 and 30 mm in length averaged 348 sq. m, and in October 1954 the same year-class, now between 25 and 35 mm in length after a summer's growth, averaged 86/sq. m, a mortality of 75% during the latter half of the winter of 1953-54 and the summer of 1954. In April 1955 the size group 25-35 mm, there being no growth during the winter months, averaged 17/sq. m, a mortality of 80% between October 1954 and April 1955. The observed mortalities of the total population (all sizes) for the same periods are: January to October 1954, 64·6%, and October 1954 to January 1955, 73·8%.

PREDATION

From the foregoing data a calculation of the mortality due to the predation of the oystercatcher can be made. This is only attempted for the winter 1954-55 as the estimates of the numbers of birds present in the previous winter are considered to be too inaccurate for this purpose. In the following calculations it is assumed that food intake during the hours of darkness was the same as during the day. We have seen already that the birds fed throughout the low tide period from and until a level of 2-2½ h ebb. Therefore they spent some 15 h a day feeding on the beds. From this and the calculated hourly food intake rates we obtain daily food intake rates of 315 cockles per day for January 1954, and 214 cockles per day for October 1954.

The estimated numbers of birds during the winter 1954-55 ranged from 25 000 - 30 000 in October to 36 000 - 37 000 in February. A figure of 30 000 will be used below. The numbers of cockles eaten per day in October 1954 therefore amounted to 214 × 30 000.

A survey of the beds in December 1954 showed the area bearing cockles to be approximately 13 square miles. An average figure of 86/sq. m, or 72 sq. yd, for the 1951 year-group only, gave a total population of such cockles of 13 × 1760 × 1760 × 72. The percentage predation per day was therefore (214 × 30 000 × 100)/(72 × 13 × 1760 × 1760) = 0·22% of the 1951 year-group. In October 1954 the total cockle population averaged 130/sq. m (109 sq. yd) which gives a daily predation rate for the total population of 0·15%. The flocks of birds are present in the area from September to March, a period of some 150 days. The mortality due to their predation during this time would therefore be 21·9% of the total population and 33·15% of the 1951 year-group. These figures should be compared with total observed mortalities, during the same period, of 73·8% of the total population and 80·2% of the 1951 year-group.

The opened shell counts of October 1954 allow an estimate of predation rate. On the first day the counts averaged 4 shells per 25 sq. yd in 2·5 h feeding, *i.e.* 24 shells/day in 25 sq. yd, a predation rate of 1·4% of the 1951 year-group. On the second day, 1515 cockles opened in 18 700 sq. yd in 2 h gives a daily predation estimate of 0·88% for the 1951 year-group. These figures, considerably higher than those calculated above, must be corrected for the density of the birds in the test area; 30 000 birds distributed over 13 square miles would on average occupy 1300 sq. yd each, whereas on the two days above each bird occupied 277 and 328 sq. yd. When the corrections are applied the figures for predation rate become 0·291% and 0·15% per day, which agree well with the figure above of 0·22% per day for the 1951 year-group derived from the population surveys. These predation rate estimates do not necessarily apply to all levels of the bed as the time that an area is uncovered decreases as the lower levels are reached. The figures are necessarily averages, bird predation probably being more severe in the upper levels of the bed. The effect of other, marine, predators would be graded in the reverse direction.

II. BRANCASTER HARBOUR

At Brancaster Harbour, the scale of the whole situation is very much reduced and observations were less detailed than at Morecambe Bay, but a useful comparison may be made. The cockle bed on which the birds were feeding in 1954 and 1955 was situated in the outer harbour, some 100 yd down the steeply shelving beach, and was small, not more than ½ mile long and some 200-300 yd wide. Running through the bank and inshore of it there was a wide, deep drainage channel, which had an important influence on the feeding of the birds. Owing to the small size of this bed and the comparatively few birds feeding on it, observations were made on the whole area and on all the birds present. The methods of observation were the same as those used in Morecambe Bay.

The cockle bed is available to the birds 2 h after high water when they commence feeding. Feeding takes place almost wholly in the shallow water at the edges of the gutter. After 2 h feeding the birds leave the bed and flock on the lower parts of the harbour, where no food appears to be taken. The behaviour on the rising tide is the reverse of this and high tide periods are spent on the salt marshes of the inner harbour. Feeding in the shallow water was as described for similar conditions in Morecambe Bay. After a few vigorous thrusts the cockle was carried to the uncovered bank and cleaned there. No damage to the shell occurred and feeding rates were very high. Some few cockles were obtained from the uncovered sand of the bank. These were opened as described for Morecambe Bay by pressure thrusts and suffered a fracture of one valve.

Observations on feeding rate and percentage of birds feeding were made on two consecutive days in March 1954, and the general description of behaviour confirmed by another visit to the area in November 1954. Feeding rate observations were made from the high water mark by telescope, the birds showing no reaction to the observer. The entire population of birds on the beds, 400-500, was used as the basis for percentage feeding counts. Nine individual birds were used for feeding rate estimations and counts of the percentage birds feeding were made every 30 min. Fig. 7 shows the results obtained. All the birds were feeding at a rate of over 2 cockles/min 2 h after high water. This rate and the number of birds feeding decreased until all the birds had left the area 4 h after high water. In the 2 h of feeding the birds spent on average half the time feeding at a mean rate of 1 cockle/min, an intake for this period of 60 cockles, and, for the tidal period, of 120 cockles per bird.

No food other than cockles was observed to be taken, although after leaving the bed at low tide periods the birds flocked on an area where alternative food was plentiful. The size-range of the cockles taken in the gutter is shown in Fig. 7, compared with the size-range of the cockle population. The mean size of cockles taken was 28·6 mm. From Fig. 6 we obtain a volume of 1·68 ml for this size, and an intake volume of 201·6 ml per bird for the tidal cycle. These figures compare well with 151·2 ml and 194·6 ml for volume intakes per tidal cycle in January and October 1954 respectively at Morecambe Bay.

The average figure of 180 ml of food taken per tide or approximately 360 ml per day gives a daily food intake of 360 g if we assume the specific gravity of cockle meat to be unity. The percentage dry weight of shellfish meat is about 25 (H. A. Cole, personal communication based on cockles from Penclawdd, December 1955, and observations by the writer on mussels at Conway, December 1955). This gives a daily food intake of 90 g, which, with a body weight of about 500 g, is 18% of the birds' own weight per day. Lack (1954) summarizes the literature on food intake of birds, most of which was obtained from laboratory studies where activity was at a minimum; 'Thus land birds weighing between 100 and 1000 g tend to eat about 5-9% of their body weight of food each day.'

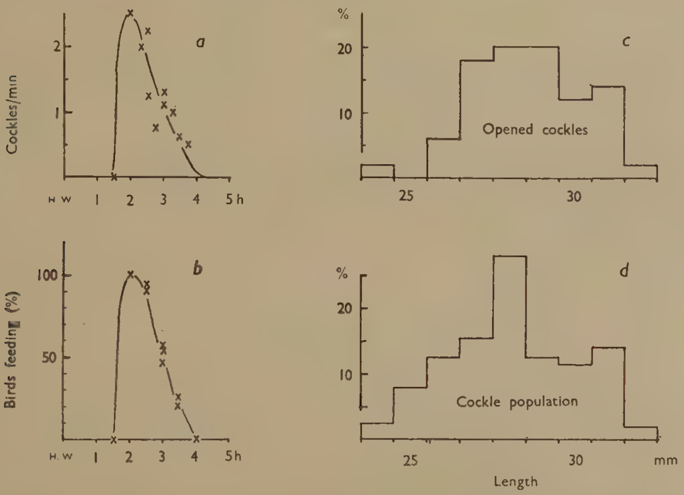


Fig. 7. Brancaster Harbour: *a*, variation of feeding rate with tidal cycle; *b*, variation in percentage birds feeding with tidal cycle; *c* and *d*, size distribution of opened cockles and cockle population in millimetre size-groups expressed as percentage total sample.

However, such figures are very approximate, varying with weather and food, and a comparison is difficult. Colquhoun (1951) reports that captive pigeons, birds of much the same size as oystercatchers, ate some 9% of their own weight of wheat per day. As Colquhoun points out the consumption of a bird in the wild is probably far in excess of this. Studies on birds in the wild are very few and, as the foods vary enormously in value, comparison is difficult. In view of the extreme activity of the oystercatcher 18% of the body weight taken as food per day compares well with published estimates on other birds.

Some few cockles were opened on the banks and a random sample collected there ranged from 24-28 mm in length, *i.e.* smaller than those from the gutter. Birds under observation on the bank were seen to desert cockles after unsuccessful attempts at opening. It is suggested that the increased effort required to open a larger cockle when tightly closed caused this bias. Whether in fact under these conditions at Brancaster the force required to open such a cockle was limiting, though cockles of the same size were opened in the Morecambe Bay area in similar conditions, or whether some 'loss of interest' by the birds, dependent perhaps on the time required for opening or on the state of hunger, was involved, is not clear.

No data were available on the cockle population, apart from the size distribution, measured by hand sieving all the cockles in a small area, and an estimate of 120-130 cockles/sq. yd derived from this. All the cockles in this sample were entering their fourth year, the result of a dense spatfall in the area in 1951 which has not since been repeated. No estimate of predation can be made, but a comparison of the relative concentration of birds at Brancaster and Morecambe Bay, suggests that the Brancaster rate would be the higher. However, other sources of food are abundant and may be utilized at other periods of the year.

When compared with the results obtained at Morecambe Bay there was a close similarity in most aspects of the feeding behaviour. The one outstanding difference was in the time required to obtain the same amount of food. The physical conditions at Brancaster make the cockles readily available and so allow an exceptionally high feeding rate.

DISCUSSION

(*a*) *Some general considerations*

The underlying purpose of this investigation into the predation of the oystercatcher on commercial cockle beds was to provide information relevant to the possible control of the birds in such areas. Though a discussion of the desirability of such control would be out of place in this paper, a survey of the knowledge necessary for reaching a decision on control measures is relevant.

Exploitation of natural populations for human food leads inevitably to a consideration of the effect of natural predators. The investigation of Davies (1955) into the bird predators of the pilchard in South Africa is an example, while White (1939) and Elson (1950) describe the effect of bird predator control on the salmon yield of the Margaree river in Nova Scotia, following a detailed study of this predation (White 1936). Apart from the possible complication of economic factors, the biological relationships in such a problem may be complex. Davies (1955) lists the requirements necessary to the understanding of a general prey-predator relationship. These are:

1. The general biology of the prey species in broad outline at least, and in particular information on the season of reproduction, development, rate of growth, feeding and migration.
2. The composition of the prey population in relation to size, age and numbers.
3. The general biology of the predator species in broad outline, and in particular

information on the season of reproduction, development, rate of growth, feeding and migration.

4. The composition of the predator population in relation to size, age and numbers.

Though this list is a full one it does not include all the factors relevant in the present study, and some of the observations included would be unnecessary. The same is found for the other studies cited in this paper, a few amongst the many prey-predator situations. In any particular study the relative importance of any of the factors listed by Davies will vary, and each case must be considered separately. Any list of requirements, such as Davies's, would inevitably, if it were to cover the relevant factors in all possible cases, be inclusive of all details of the ecology of both prey and predator species. The scope of such a list would render it valueless, by the very virtue of its general applicability.

In place of such a list the broad principles of investigation may be stated as follows. Basically, to estimate the importance of predation the mortality of the prey population due to that predator must be related to the total mortality from all causes. If the mortality due to a predator is known only in absolute terms, the relative effect on the prey population of removal of this cause of death, even in its crudest form, is unknown. Though apparently of importance in absolute terms, such a mortality may in fact be insignificant when compared to the total mortality. In the case of an exploited prey population, where the annual commercial catch is confined to an arbitrary limit not based on scientific data, as in the case of the South African pilchard fishery, the relationship between predation and total mortality loses its importance, but is a basic essential for the understanding of prey-predator relationships in general.

Further, in forecasting the effects of predator control, as much as possible of the mechanics of the ecological system of which the prey and predator species form a part must be known. The work of Steven (1933) on the food of shags and cormorants provides an example of the danger of too limited an appraisal of the predator-prey relationship. This worker, in discussing the method of assessing the gut contents so as to measure the usefulness or otherwise of a bird in question, cites the case of a cormorant which was found to have eaten fifteen small flatfish. Steven continues: 'The combined volume of all these fishes was less than that of a fully grown adult. But they would have produced fifteen adult marketable fishes had they been allowed to live. By destroying these young individuals therefore this particular bird had done quite as much potential harm to the fish stock as if it had eaten an equal number—or over twenty times the volume—of adults.' The underlying assumption that predation by the cormorant is the sole or even a major source of flatfish mortality is unwarranted and almost certainly untrue.

Any attempt to regard the situation studied as static can lead to very wrong conclusions. In addition to any possible change in relationship with time, the repercussions of the removal of a component of the ecological system must be considered. A minimum further requirement would be detailed knowledge of the mortality of the prey, in terms of other causes of death, and the food of the predator. White (1939) in his report of the result of bird control on survival of salmon provides an excellent example of possible complications in this connection. The removal of bird predators was found to increase the number of salmon in the river, but at the same time allowed the survival of more large trout, also preyed on by the birds, and these trout fed on the young salmon. As White notes 'even though bird control increases the salmon of the Margaree, it does not follow that such control is desirable for all salmon streams'. In the Margaree river, trout numbers are controlled by angling, but where this is not the case, any benefit from bird control would be lessened and might even be negated by trout increase.

The above is necessarily a very brief account of a complex subject and no claim is made for a review of all the possible ramifications, but rather an attempt at a logical and realistic approach to the basic principles of the problems of predator control.

(*b*) *Oystercatcher predation*

At first sight the data presented above would lead us to expect at Morecambe Bay an increase of over 80% in the cockle population surviving the winter of 1954-55 if all oystercatcher predation had ceased in 1954. This estimate, however, suffers from the serious error of regarding the situation as a static one and disregarding any interaction of relevant factors. From the point of view of forecasting the effects of oystercatcher control this may be a grave omission. Though any indication of such sources of error must at this stage be hypothetical, the following are suggested.

The total annual mortality experienced by the cockle population in Morecambe Bay (74%) is seen to be far in excess of that estimated to be due to oystercatchers (22%). Gathering by cockle fishermen continued throughout the period but this take-off was estimated to be far less than that of the birds. Flatfish may well account for a considerable proportion of the balance, as plaice and flounders are abundant on the banks and undoubtedly feed on cockles. Todd (1914) states, for the North Sea, 'Mollusca are the chief source of food for fish [plaice] over 15 cm'. Jones (1952) studying the food of flatfish off the Cumberland coast, found lamellibranchs to be the principal food of both plaice and dabs. It is possible that a relation between predator numbers and prey density, such as suggested below for the oystercatcher, holds for fish predators too, in which case the benefit from oystercatcher control would be modified by this factor. An increase in the population density of cockles would lead to an increase in the numbers of fish predators and hence their predation.

The application of the data to any period other than that studied has its dangers too. The relationship between the numbers of oystercatchers and cockles may well be a complex one. A feature of cockle beds in general is the irregular nature of the recruitment. A gap of several years typically occurs between dense settlements of young cockles. Such a situation was evident on the two beds treated in this paper. The relationship of the size of the oystercatcher flocks to varying food populations is not well known, but Dr E. Duffey (in a private communication to

Mr E. M. Nicholson, kindly made available to me) describes a dense settlement of cockles in Brancaster Harbour on the site of the observations detailed above, in 1947-48. This was followed by an increase in the oystercatcher population to a maximum of 3000-4000 in 1950, far in excess of the numbers found during the survey period. As the cockle population declined in succeeding years so the oystercatcher flocks returned to normal. Lack (1954) cites examples of such prey-density-dependent fluctuations of predator species. The decline in numbers of the oystercatcher flocks in Morecambe Bay during the two years' studies may well be a similar case, and a nomadic habit of winter flocks, with the exploitation of local food abundance, may be a feature of oystercatcher behaviour. If so, then any forecast of predation in years following the actual survey period must depend on a knowledge of the relationship between cockle density and oystercatcher numbers.

To provide reliable answers to questions such as these, would require detailed investigation over a number of years. The desire for perfection of knowledge must, however, be balanced against the value of the fishery and the possible harmful effects of continued uncontrolled predation.

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SUMMARY

1. An investigation into the predation of the oystercatcher (*Haematopus ostralegus*) on the edible cockle (*Cardium edule*) covering the winters of 1953-54 and 1954-55 is described. Two areas were studied, Cartmel Wharf in Morecambe Bay on the coast of Lancashire, and Brancaster Harbour on the north coast of Norfolk.

2. In Morecambe Bay large flocks of birds visit the area in winter. Their origin is discussed and the suggestion made that they come from northerly breeding areas outside Great Britain.

3. The birds show a rhythmic feeding movement within the area, corresponding to the tidal cycle, and this continues during darkness.

4. The feeding behaviour of the birds and the method of gaining entry to the cockle are described. The importance of the size of the cockle and the physical properties of the substratum are illustrated.

5. From field observations estimates of food intake of 315 cockles 20-30 mm in length per day in January 1954, and 214 cockles 25-35 mm in length per day in October 1954 are reached. The analysis of gut contents of birds killed on the survey showed these estimates to be well within the digestive capacities of the birds.

6. From observations of feeding birds and gut analysis it was found that *Cardium* was the main source of food though the other invertebrates found on the beds were taken occasionally.

7. A photographic method of flock estimation gave estimates of 30 000 - 37 000 birds on the Cartmel Wharf cockle beds in the winter 1954-55.

8. The cockle population is described from sieved samples and a total mortality of 73·8% in the winter 1954-55 is shown to have occurred.

9. The predation due to the oystercatcher flocks is calculated as 21·9% of the total cockle population for the winter of 1954-55.

10. The results of an investigation at Brancaster are compared with conditions at Morecambe, the only important difference being that the feeding conditions at Brancaster allow a higher feeding rate and result in the birds spending less time in feeding. The amounts of food taken in the two areas compared on a volume basis did not differ greatly.

11. The knowledge necessary for a clear understanding of any prey-predator relationship is discussed and illustrated by reference to the subject matter of the present paper.

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THE BEARING OF PARASITE BEHAVIOUR ON THE DYNAMICS OF INSECT HOST AND PARASITE POPULATIONS

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The population dynamics of parasitic insects and their hosts has scarcely been studied in the field in spite of its importance in the understanding of the success or failure of biological control. In purely theoretical studies Nicholson & Bailey (1935) assumed that a female parasite had an unlimited egg supply but a fixed and limited searching ability which they call its 'area of discovery'. This they consider to be constant in a constant environment under all combinations of host and parasite population densities. The number of hosts attacked by a female parasite must therefore be related to host population density. They further assume that the searching of the population is random. On the basis of these assumptions they obtain formulae which express what happens when a population of one parasite species interacts with a population of a single host species.

If H_n represents the number of hosts in the n^{th} generation, and the coefficient of increase is f, then in the next generation the number initially present in the unit area is fH_n. The surviving number in the $(n+1)^{th}$ generation remaining undiscovered after the area has been searched by P_n parasites,

$$H_{n+1} = fH_n e^{-aPn} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

Moreover, since each host discovered gives rise to one parasite in the next generation, the changes in the parasite population are given by the formula

$$P_{n+1} = fH_n - H_{n+1} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

Theoretically a steady state could occur in which the population densities of both host and parasite would be the same in successive generations. But any disturbance of this state of balance should set up oscillations in population density which increase in amplitude in successive generations, even in a constant environment.

These theoretical studies have had considerable influence on thought, but they have been subjected to insufficient critical analysis. De Bach & Smith (1941*a*) attempted 'to determine experimentally whether these formulae describe approximately the course of events when a host and parasite population interact, the generations being distinct'. They concluded that 'so far as the experiments have gone they lend strong support to the idea that population oscillations are inherent in the host-parasite or predator-prey interaction'. Opinions vary greatly as to the weight of this support; the conclusions are not accepted by Andrewartha & Birch

(1955) but are quoted without adverse criticism by Allee *et al.* (1949) and Utida (1950). Utida (1955) has also published graphs showing oscillatory population changes in the continuous interaction between *Callosobruchus chinensis* (L.), the azuki bean weevil, and its braconid parasite *Heterospilus prosopidis* Viereck.

In this present paper the experiments of De Bach & Smith are re-examined, their results are analysed further and are interpreted in the light of recent work on the physiology and behaviour of the parasite used.

THE EXPERIMENTS OF DE BACH & SMITH

Nicholson & Bailey's theory does not lend itself readily to a critical experimental analysis. Assumptions introduced to simplify the mathematical processes complicate the biological aspects; for example, it is assumed that the life cycles of host and parasite are synchronized. It would be difficult to find host and parasite species for which this is exactly true. Under constant laboratory conditions synchronization is probably unattainable. De Bach & Smith devised experiments which overcame these difficulties. Populations of known numbers of the chalcid wasp *Mormoniella vitripennis* (Walker)* were allowed to search in the dark at 80° F for known numbers of house-fly puparia aged three days and of standard size which had been evenly distributed amongst three quarts of barley in a ten-gallon tin. 'The parasites used were all four days old, were previously fed honey and had not been allowed to oviposit.' They were left in the tin for 24 h, after which the puparia were sieved out of the barley and examined. The proportion of available time spent in searching was not observed, but uncontrolled variations in parasite longevity were avoided by limiting the period available for searching. Each period of 24 h was treated as a 'generation'. The number of hosts parasitized in each 'generation' was counted and that number of parasites was used in the next 'generation' and allowed to search for more standard hosts whose number was twice that of the survivors of the previous 'generation'.

De Bach & Smith followed this routine for seven 'generations' and thus constructed an experimental model in which the generations of host and parasite were exactly synchronized, the host's reproductive rate was fixed artificially at two, a single female parasite arose from each parasitized host, and mortality of other kinds in the intermediate stages was eliminated. De Bach & Smith were thus able to put values for parasite and host population densities in equation (1) and calculate the value of the area of discovery a, for the conditions of the experiment. Then using equations (1) and (2) they calculated the population densities for host and parasite for thirteen successive generations. The curve for the calculated population was compared visually with that obtained for the seven experimental generations. They concluded that 'the populations of both host and parasite followed closely the theoretical predictions of Nicholson & Bailey through seven generations'.

Andrewartha & Birch (1955, p. 443) claim that these experiments do not serve as an empirical test of the Nicholson & Bailey model, since 'all premises of the model were supplied arbitrarily by the design of the experiment'. This is untrue. All variables were controlled with the exception of the searching ability of the parasite, which the experiment was in effect designed to investigate.

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* This species has often been called *Nasonia brevicornis* Ashmead, and is referred to as *Nasonia vitripennis* (Walker) by Muesebeck, Krombein & Townes (1951).

THE PHYSIOLOGY AND BEHAVIOUR OF *MORMONIELLA VITRIPENNIS*

The interpretation of an experiment in which a parasite is given the opportunity to search for a suitable host species requires some knowledge of the variation in the proportion of time which a parasite spends searching for new hosts under different circumstances, and in particular how it is influenced by the density of host and parasite populations. A brief outline of the physiology and behaviour of *Mormoniella vitripennis* is given here (see Edwards 1954*a* and *b* for a fuller account).

When a female emerges from its pupal skin within the puparium of her dipterous host, the fat body is large and the ovaries contain no mature eggs. The newly emerged female spends 20-30 h inside the host puparium before biting her way out, and by this time the first few eggs have matured. A female which is then starved lives for 5 days only, and a maximum of sixteen eggs reach maturity at the age of 48 h. Thereafter the matured eggs are rapidly resorbed so that only two or three are left when she dies. If the female is supplied with honey, 25 eggs are present on the third day, and the number present falls gradually because resorption takes place slowly, and the number of eggs is almost maintained by the maturation of one or two more every day. In the case of very small females the maximum number of mature eggs never exceeds eight.

When females are allowed to oviposit on hosts they form a feeding tube and suck up some of the host blood. The protein-rich diet accelerates egg maturation, and the ovaries soon contain as many as thirty rapidly developing oocytes in addition to twenty mature eggs. When females have had only honey for the first 48 h of life this maximum rate of egg production is not reached until 3 days after the provision of a blood diet. The fat body has by this time disappeared, and if such females are starved oosorption is extremely rapid, and death may occur within 48 h. If fed on honey females survive, and the total number of eggs in the ovaries decreases slowly as before.

The odour of food on which fly larvae have been feeding may affect the behaviour of *M. vitripennis*, but the parasite is unaware of a fly puparium in the dark until it is actually touched with the antennae. Once found, the puparium is investigated with the antennae and a hole drilled with the ovipositor, taking between 15 min and 1 h. If the host is suitable, eggs are laid and a feeding tube is formed taking another 30-40 min, depending on the number of eggs laid and the amount of food taken. After a period of resting and cleaning the cycle of behaviour may be repeated before the parasite finally leaves the puparium. When females have been deprived of hosts and contain few mature eggs, a particularly long period of resting and cleaning follows oviposition. As much as 20 h may be spent on the same puparium, even though others suitable for oviposition are lying nearby.

DISCUSSION

De Bach & Smith claim that their experimental curve closely follows that predicted by Nicholson & Bailey's theory, but as there is no suitable method by which the goodness of fit can be examined statistically, this must remain a matter for subjective judgment. A more rigorous test is to see if the experiments confirm one of the fundamental assumptions of the theory—that the area of discovery remains constant. De Bach & Smith (1941*b*, 1947) carried out two other series of experiments using the same parasite and host species over a wider range of population densities. The aim of the experiments was different, but the experimental procedure was precisely the same, so it is permissible to evaluate and compare the area of discovery in all three series of experiments (Table 1).

Table 1. *The 'area of discovery' of* M. vitripennis *together with the number of hosts found per parasite for various combinations of host and parasite density*

	Data from De Bach & Smith			Calculated	
		Host Density			
	Parasite Density	Initial	Final	Hosts found per parasite	Area of discovery
1941*a*	18	36	15·4	1·15	0·047
	21	31	12·9	0·86	0·042
	18	26	11·0	0·78	0·048
	15	22	11·3	0·60	0·044
	11	23	14·3	0·79	0·043
	9	29	18·3	1·2	0·051
	11	37	23·5	1·2	0.041
	14	47	–	–	–
1941*b*	40	1	0·111	0·025	0·055
	40	5	1·00	0·1	0·040
	40	25	7·43	0·5	0·030
	40	50	18·5	0·75	0·025
	40	100	51·7	1·25	0·016
	40	200	146·0	1·3	0·008
	40	300	238·0	1·5	0·006
1947	5	40	31·6	1·7	0·047
	25	40	18·9	0·84	0·030
	50	40	8·8	0·63	0·030
	100	40	1·8	0·38	0·031
	200	40	0	0·25	∞
	300	40	0	0·13	∞

In the 'oscillation' experiment (1941*a*), with the host numbers in the seven generations ranging from 22 to 47, and the parasite numbers from 9 to 21, the calculated area of discovery of the parasite (taking the area of the environment as unity) ranges from 0·041 to 0·051; in the series of experiments with 40 hosts (1947) and parasite numbers from 5 to 100, it varies between 0·046 and 0·030; but when the parasite numbers are higher, no hosts escape and the area of discovery is infinite. When host numbers are increased from 1 to 300 (1941*b*) and parasite numbers remain at 40, the area of discovery diminishes from 0·055 to 0·006. Thus under the conditions of the experiments, the value of the area of discovery remains approximately constant over the lower ranges of host and parasite densities, but rises towards infinity when parasite densities are high, and falls to low values when the host density is high.

Even when host density is high in relation to parasite density, it is a striking fact (Table 1, column 4) that the success of the parasites' searching is very low. The mean number of hosts found per parasite does not exceed 1·7 (when 5 parasites search for 40 hosts) and is usually a little over 1·0. This poor performance is not due to the hosts being concealed, but to the previous history of the parasites. If four-day-old females which have been fed on honey are confined for 24 h with numerous puparia in a 3 in. × 1 in. tube they will parasitize only one or two hosts, whereas females which have previously been fed on host blood may parasitize as many as twelve in 24 h. Hence the effect of depriving the parasites of hosts is not, as might have been expected, to increase the searching drive. Instead it limits their ability to attack more than one or two hosts during the succeeding 24 h period. Thus De Bach & Smith's arbitrary choice of four-day-old parasites fed on honey was particularly unfortunate, for such females cease searching for many hours after the discovery of the first host, and having very few eggs in the ovaries soon reach the limit of their egg supply. This is contrary to the conditions assumed in the Nicholson & Bailey model, but is in agreement with the assumption made by Thompson in his theoretical studies. (Thompson 1924, 1939 for a fuller account.)

If insect parasites have a limited egg supply, when host density is high they can find more hosts than they can parasitize, so the calculated area of discovery will be low. This explains the results of De Bach & Smith's experiment (1941*b*).

Mormoniella vitripennis can survive without food at 25° C and 75% R.H. for only 2 days. Each host it finds provides food, and thus extends its life, and hence its ability to search for more hosts. When host density is so low that a host is not found in 2 days, the parasite will die of starvation unless it turns to some other source of food such as honey dew or nectar. But if a parasite delays finding a host, the number of eggs in the ovaries is reduced, and more time will be spent in feeding on the next host found. Thus the area of discovery will be reduced by low host density.

Under natural conditions we must suppose that with increasing host density the area of discovery would at first rise to a maximum, and subsequently decrease again to a low level at very high host densities. This complex relationship between parasite longevity and host density was eliminated by the design of the De Bach & Smith experiment.

De Bach & Smith demonstrated the beginning of oscillations of the type predicted by Nicholson & Bailey, but the reduction of the area of discovery at high host density to which we have called attention would have caused a serious deviation from the calculated curves had the experiments continued for another 'generation' or two. Their results were nevertheless interpreted by them as supporting the idea that oscillations were 'inherent' in the parasite-host interaction. That they occur in similar experiments has recently been confirmed by two separate communications to the Tenth International Congress of Entomology at Montreal in 1956. Dr T. Burnett of Belleville (Ontario) used the white fly *Trialeurodes vaporariorum* Westwood, and its chalcid parasite *Encarsia formosa* Gahan which he was able to follow through twenty-two artificial 'generations' in which all variables were controlled save parasite searching ability. He found oscillations of increasing amplitude with peaks every eight 'generations'. Dr Luiz O. T. Mendes of Brazil reported similar experiments using the larva of the flour moth, *Ephestia kuehniella* Zeller as host and the parasite *Idechthis* (=*Nemeritis*) *canescens* (Grav.) as parasite. Until the results are fully published and the behaviour of these insects has been described in detail, analysis is premature. According to formulae (1) and (2) the oscillations in population density increase so rapidly in amplitude that in an environment as small as those used in these experiments extinction would be the consequence after three or perhaps four oscillations. Whether the theoretical or the observed oscillations are therefore to be termed 'inherent' is open to doubt. However, the important conclusion that population oscillations *can* occur in constant climatic conditions is itself of sufficient importance.

Possible ways in which oscillations might be 'damped' or 'quenched' were considered by Nicholson, and have since been studied by others, such as the late Dr L. Tinbergen (see Varley & Gradwell (in the press)). Long continued though rather irregular oscillations have been reported by Utida, who has kept a variety of stored product insects with their hymenopterous parasites in small environments. It is not the purpose of this paper to analyse his findings critically; in the absence of sufficient information about parasite behaviour, and because his experimental conditions were quite unlike those studied here, a similar analysis is not practicable.

We hope that there will be many further attempts to study the interaction of parasites and their hosts both in the field and in the laboratory; but it must be emphasized that a suitable experimental design, and the proper interpretation of results both require detailed knowledge of parasite behaviour.

SUMMARY

1. The behaviour of the Chalcid wasp *Mormoniella vitripennis* towards its host is described. Females previously deprived of hosts are unable to parasitize more than two hosts in 24 h.

2. The experiments of De Bach & Smith are critically re-examined. Their results are used to calculate for *M. vitripennis* the 'area of discovery' assumed by Nicholson & Bailey to be a constant.

3. Over much of the range of host and parasite population densities studied the calculated area of discovery is reasonably constant, but falls to very low values when the host population density is high.

4. At high host population density the number of hosts attacked by each parasite is independent of host density, and the situation fits the theoretical model of W. R. Thompson more closely than that of Nicholson.

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THE DISTRIBUTION OF INSECTS IN THE AIR AND THE EMPIRICAL RELATION OF DENSITY TO HEIGHT

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(With 2 Figures in the Text)

INTRODUCTION

The knowledge that insects are found at great heights in the air has not been satisfactorily incorporated into the general picture of insect ecology. I think that there has been a tendency by most entomologists to suppose that the upper air, above say 200 or 300 ft, occasionally receives a relatively small proportion of unfortunate individuals which manage to become separated from the main population, and that if they do not die by being swept aloft they are probably of doubtful importance compared with those denser populations visible nearer the ground. This point of view assumes that the lower layers of the air, with their insects, remain more or less distinct from the upper levels. This is in general not so. The whole aerial population is best regarded as a continuous diffusion system in which there is continual exchange, both upwards and downwards, of all the individuals in the various layers of the atmosphere up to high altitudes, and that this is not an occasional event but goes on most of the time. To subdivide the atmosphere into 'terrestrial' and 'plankton' zones as Berland (1935) and others have done therefore tends to be misleading. This idea will probably run counter to those held by entomologists familiar with larger species, such as moths, butterflies, bees or large diptera, where often the same individuals can be seen keeping their own position relative to the ground. But the vast majority of alate individuals are very small and do not come into this category, which in any case often breaks down, and dispersal by way of high altitudes (*i.e.* at least hundreds of feet) happens at least once in the lives of most alate individuals and species found flying over open country.

Misunderstanding and the technical difficulties in studying dispersal in the upper air have led to its neglect; but the earlier work up to about 1945 on high altitude dispersal tended to run into a blind alley for another reason, and incidentally to divorce this subject from its terrestrial and ecological context. The main interest was at first in the kind of weather in which more or less drift occurred, and so direct correlations were made of insect abundance at various heights with such factors as the temperature, humidity, wind and pressure at the time of capture. This approach could not lead to an analysis of the dispersal process. For the number of insects at a particular height depends firstly on the size of the terrestrial populations from which they come, and this is not dependent on current weather;

secondly on the proportions taking flight, which though associated with weather is not simply correlated with it (Johnson 1954); thirdly the numbers at a given altitude depend also on the way in which the aerial population is distributed between various heights, and this is largely a matter of atmospheric stability and not easily expressed in terms of temperature, humidity or wind at any particular height. The subject has thus to be resolved into two aspects: the relative abundance at different heights irrespective of actual densities, that is the density-height gradient, a problem of diffusion and displacement; and the variation in total numbers in the air, a problem of population change and of the proportion flying.

This paper deals with the first aspect. It will be shown that the density at various heights is not a capricious arrangement but that there is usually a profile in which density diminishes with height; and though subject to the vagaries of wind, weather and flight behaviour, this profile is in general capable of precise formulation. The paper is in in three parts: the formulation of an empirical equation for the general relation of insect density to height; the integration of this expression to give a means of estimating the total numbers of insects in a zone of air between any two heights; and the fitting of the empirical formula to all relevant data. This empirical approach has been the first step in an analysis of the distributive process. A second paper in collaboration with Mr J. G. Skellam will seek to interpret the relation of insect density to altitude in terms of diffusion theory and to assign biological and physical meaning to the parameters in the empirical equation.

THE GENERAL FORM OF THE VERTICAL DENSITY PROFILE

Insects take to the air, become dispersed through it and return to earth. The relative rates of these processes determine the form of the vertical distribution in which density usually diminishes with height in the form of a hollow curve. The distribution is not to be thought of as a static arrangement but as different individuals continually replacing each other at different heights. It may remain more or less the same for a considerable period, however, by a steady balance in the rates of take off, landing and upward and downward diffusion by flight, turbulence and convection, or it may change its form rapidly by alteration in the rates of one or more of these processes.

(*a*) *The empirical approach to the relation of density to height*

Formerly differences in the aerial densities of insects up through the air had been expressed as a ratio of any two densities, or the aerial situation had been described in words, but in 1946 Wolfenbarger produced an empirical semi-logarithmic formula to fit both Hardy & Milne's (1938) and Freeman's (1945) data; he was, however, unable to find a satisfactory expression for Glick's (1939) figures which were then the most extensive available on vertical distribution. Later Johnson & Penman (1951) found that with aphids log density was linearly related to log height only beyond a certain height above the ground.

The formula described in the present paper, however, fits most of the data. It possesses the practical advantages of being easily integrated to give the total aerial population, it provides a useful linear transformation of density on height, and it expresses the whole profile quantitatively with a single parameter, λ, so assessing the relative proportions higher or lower in the air. The formula is thus useful ecologically apart from providing a point of departure for a further and more functional analysis. It is convenient to begin by considering the simple relation of density, $f(z)$, on height, z, when density × height to the power λ is constant:

$$\text{thus } f(z).z^{\lambda} = C,$$

though this does not hold good in nature. When $\lambda = 1$ the reciprocal of density is linearly related to height; that is

$$\frac{1}{f(z)} = \frac{z^{\lambda}}{C}$$

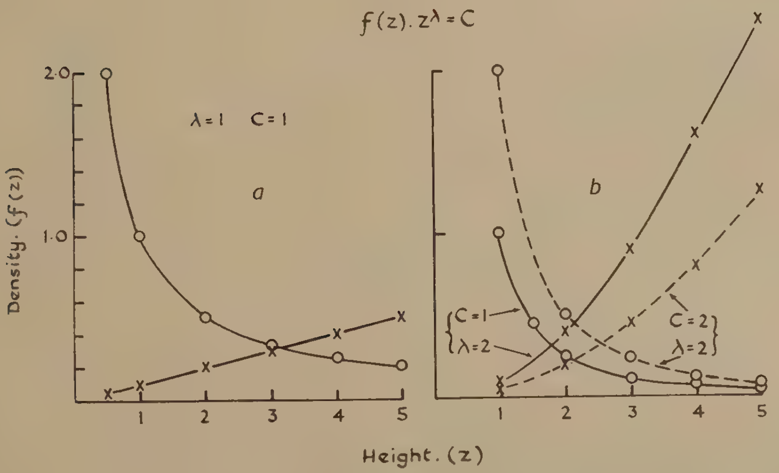

Fig. 1. Hypothetical density-height curves, with different values of λ and C, obeying the expression $f(z).z^{\lambda} = C$.

These relations are illustrated in Fig. 1*a*. If height was doubled (*e.g.* from 2 to 4 or from 8 to 16) the density would be halved. If, however, $\lambda > 1$ the graph of $\frac{1}{f(z)}$ on z is curved: thus if $\lambda = 2$ doubling the height (from any origin) quarters the density (Fig. 1*b*). λ is thus an index of the diminution of density with height and of the balanced rate of upward and downward diffusion. The position of the curve is, however, determined by the general size of the aerial population. Thus if the population was doubled at each height, λ remaining the same, then although doubling the height would halve or quarter the density, this is done from different total population levels (as distinct from different densities on the same curve).

This is illustrated in Fig. 1*b*. Thus if all other factors were to remain constant, doubling the whole population would double C. C on the other hand is not a simple index of population level unless the other factors are held constant. It is possible therefore to obtain many curves of $f(z)$ on z for different values of λ arranged at different heights along the ordinate according to different values of C.

Vertical distributions in nature do not, however, conform to the formula $f(z).z^{\lambda} = C$, though sometimes they very nearly do, for it implies an asymptotic relationship, density reaching an infinitely great value just above the ground and an infinitesimally small one at an infinite height. Actually density is finite near the ground and is probably limited in degree as well as in height by the convection top. If, however, the ordinate is shifted to the left until the observed curve, when extrapolated, becomes asymptotic with it, then the equation for the curve becomes

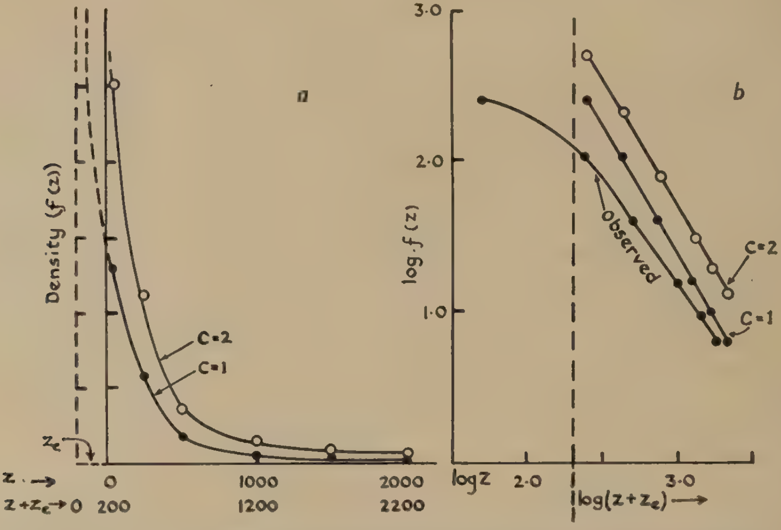

Fig. 2. *a*, Two curves of density on height for the same value of λ but different values of C, obeying the expression $f(z).(z+z_e)^{\lambda} = C$; *b*, Double logarithmic transformation of curves in (*a*). Observed curve is not linear until z_e has been added to height.

$$f(z).(z+z_e)^{\lambda} = C$$

where z_e, the amount of displacement, is a constant added on to all the observed heights (Fig. 2). Put in a more convenient form this equation is

$$f(z) = C\ (z+z_e)^{-\lambda} \ldots\ldots (1)$$

and is the empirical equation for the assumed steady state which is found to fit most of the observed data. The parameters are:

$f(z)$ is density at height z

C is a scale factor dependent on the general size of the population in the air; it is, in fact, the expected density when $(x+z_e) = 1$

λ is an index of the profile and of the aerial diffusion process

z_e is an added constant characteristic of the data and whose significance (to be discussed in the second paper) probably depends on the rate of exchange of insects between air and ground.

When the distribution is building up or decaying, as in the morning or evening (Johnson 1956) this equation may not hold good. The number of occasions when this occurs may be appreciable during the day and night. Yet because more insects fly during the warmer periods of the day where the atmosphere tends to instability, the majority of insects will be captured when the general expression does hold good; hence its validity with most trap data.

(*b*) *The logarithmic transformation*

The expression $f(z) = C(z)^{-\lambda}$ gives a linear graph of $\log f(z)$ on $\log z$;

$$\text{that is } \log f(z) = \log C - \lambda \log z.$$

The slope varies with λ and the position with C (Fig. 2*b*). Such simple transformation of the data of density on height from nature does not, however, give a linear graph; when the origin is displaced by z_e, however, then $f(z) = C(z+z_e)^{-\lambda}$ and the graph of $\log f(z)$ on $\log (z+z_e)$ is linear (Fig. 2*b*). Thus λ is the regression coefficient of log density on $\log (z+z_e)$; it expresses the slope of the line and the proportion of insects in different zones. In this respect λ is independent of population size and of C.

In the natural data ground level or zero height becomes infinity when put into logs ($\log 0 = \infty$). It is convenient therefore to regard the lowest altitude as 1 ft which becomes 0 on the log scale. The density gradient at the ground level-air 'interface' then presents its own problems, which will be discussed in the second paper.

INTEGRATION OF DENSITY ON HEIGHT: ESTIMATING NUMBERS IN ZONES OF AIR

Given any two heights z_1 and z_2, and the values of λ, C and z_e, it is possible to estimate the total number of insects in the zone between the two heights

$$f(z) = C(z+z_e)^{-\lambda}$$

$$\int_{z_1}^{z_2} f(z).dz = \int_{z_1}^{z_2} C(z+z_e)^{-\lambda}.dz$$

$$= \left[\frac{C(z+z_e)^{1-\lambda}}{1-\lambda}\right]_{z_1}^{z_2}$$

$$= \left[\frac{C}{1-\lambda}(z+z_e)^{1-\lambda}\right]_{z_1}^{z_2}$$

Total insects between z_1 and z_2

$$= \frac{C}{1-\lambda}\left[(z_2+z_e)^{1-\lambda} - (z_1+z_e)^{1-\lambda}\right] \ldots\ldots (2)$$

The height and density increments are in feet and in number/10^6 cu. ft respectively. Therefore each height increment represents a flat plate of air 1 ft high and 1000 ft square. The integrated value between any two heights can therefore be regarded as an estimate of the number of insects in the column of air of 1000 × 1000 ft cross section extending between the two heights: but this is an abstraction. Actually it is the number of insects in a similar volume, the width of the trap influence, extending downwind for a distance determined by the speed of the wind and the trapping period; and this distance is not constant at all heights, for wind varies with height.

The ability to estimate the total number of insects in the air obviously has opened up many new possibilities especially if this estimate can be associated with the size of the terrestial populations.

FITTING THE DATA ON VERTICAL DISTRIBUTION TO THE EMPIRICAL FORMULA

In the present section the data at our disposal are fitted to the formula $f(z) = C(z+z_e)^{-\lambda}$ and the appropriate values of the constants given in the tables. As will be seen, observed and expected values are, in most instances, very close to each other.

(*a*) *Method of determining the values for* λ, z_e *and* C

The observed data of density on height are plotted on double logarithmic paper; this gives a curved graph, usually as in Fig. 2*b*. As in this figure, the observed heights are increased by a constant amount until the graph becomes straight; the amount required for this is taken as z_e.

λ and C are calculated as follows. Two points at each end of the graph are taken; often the fit is so good that the observed data themselves can be used but when this is not so, values on the line are taken. Thus if at observed heights of 50 ft and 2000 ft the density estimates are 84·7 and 2·8 respectively, then for the straight line

$$\text{Density at } 50+z_e = 84{\cdot}7$$

$$\text{Density at } 2000+z_e = 2{\cdot}8$$

$$\lambda = \log\left(\frac{84{\cdot}7}{2{\cdot}8}\right) \div \log\left(\frac{2000+z_e}{50+z_e}\right)$$

$$\log C = 84{\cdot}7+\lambda \log (50+z_e)$$

log C, is in fact the value at the intercept on the log density axis when $\log (z+z_e) = 0$.

(*b*) *General characteristics of the data*

The density measurements taken at different heights to estimate the vertical profile of insect density must be made simultaneously, and for a precise estimate a very short trapping period is desirable. This period depends in practice on the time necessary to collect samples of adequate size; so far the minimum period has been 1 h (Johnson & Taylor 1955*a*, *b*) and although Glick made 10 min sweeps at each height, these were done consecutively during one or two-hour periods. The estimate of each density, and also of the profile for a single trapping period, is therefore an arithmetic mean value with no indication of variation within the trapping period.

Ideally the density-height profile should be considered for each species separately, for it varies even between closely related species (Johnson, unpublished data). But it is often difficult to collect a sufficient number of a single species at considerable heights where densities may be very low, and many good data would be lost by such an over-refinement at this stage. A consideration of individual species has therefore been postponed, data for many species have been pooled, and mean densities obtained of a number of estimates at each height taken over a considerable period of time; the profile was obtained from these means. Obvious sources of error in such a general treatment have been accepted temporarily: for example, catches at the higher altitudes may contain a greater proportion of insects from a wider area than catches made close to the ground; the vertical distribution differs in time and from species to species, and therefore pooled data require suitable weighting which has not been possible here; the mean values of profiles have been determined over periods that are unduly long in view of the rapidity of the distributive processes. Thus, although Glick trapped for only 10 min at each height, his published data give only totals for all trappings during five years. It might appear, therefore, that such profiles for many species together, measured over lengthy time periods, have little significance. Nevertheless this general treatment has produced a helpful and indeed striking quantitative generalization with very diverse data, gathered by different methods, for different periods and for many species in different parts of the world.

All the more outstanding, suitable, quantitative data available have been considered, but some data for altitudes below about 30 ft (*e.g.* Wolfenbarger 1946) have not been analysed, firstly because the traps varied in efficiency with varying wind-speeds, and therefore with altitude, making it impossible to estimate density from the published data; secondly because at heights near the ground the flight behaviour of insects evidently plays a greater part in determining vertical distribution than it does at higher altitudes. Indeed the distribution within a few feet of the ground may perhaps be regarded as a separate study (see p. 483). Other data deliberately omitted which did not conform to the general formula are very few. They were those of Glick (1939) for collections up to 4000 ft in Mexico, those of Freeman (1946) up to 277 ft for spiders and mites, and the samples for a few hours at Cardington in 1950 and 1951. The densities on these observations did not always diminish with increase in height, and it is best to postpone their consideration until changes in the density-height gradient during the day and night are described, for on some occasions within the 24 h 'inversions' of densities are known to occur (Johnson, unpublished data). Except for some data (Table 4) all collections were made in daytime and at altitudes not less than 10 ft from the ground. The periods over which density profiles have been estimated, the method used and the insects concerned, will be given in the tables or in the text.

(c) *Data of Hardy & Milne (1938)*

Most of the sampling was done near Hull, Yorkshire, over flat country exposed to the wind from all quarters, but other sampling flights were made near the following places: on the coast at Thorpeness, Suffolk, which is flat, the 50 ft contour being 2 to 3 miles inland, the country beyond becoming undulating up to 150 ft; at Tetney, Lincolnshire, 3 to 4 miles inland over very flat, level land rising to about 300 ft 7 miles inland to the west; on the coast on the top of Abbots' Cliff (400 ft) near Dover, Kent, the land behind undulating between 250 and 500 ft above sea level.

Technical difficulties prevented simultaneous measurement of density at various heights, and the objectives of the work did not demand it. Samples were taken at different heights on different days and even in different places, and the heights were not always accurately determined; there were more frequent samples at some heights than at others. In estimating the mean insect density (Table 1) numbers caught were converted into number/unit vol. of air by using a single average wind-speed of 12 m.p.h. for all heights and times. Consequently the data are not as satisfactory as one would wish from the present point of view. Yet their analysis suggests that the order of the changes in density with height overwhelm even the errors in these data (although they are probably maximal) and permit a useful comparison with other more suitable observations. At the highest altitude the data obviously do not conform to the expected curve. But this is not surprising in view of the variation in trapping procedure; causes other than this perhaps need not be sought.

Table 1. *Data for total insects from Hardy & Milne (1938)*

Height (ft)		No. insects/10^6 cu. ft	
range	median	observed	calculated
10-150	80	87	81
150-300	225	29	31
300-500	400	18	18
500-750	625	10	11
750-1000	875	9	8
1000-2000	1500	9	5

$\lambda = -1{\cdot}0056$ $\log C = 3{\cdot}8736$ $z_e = 10$

Table 2. *Data for total insects from Freeman (1945)*

	No. insects/10^6 cu. ft	
Height (ft)	observed	calculated
10	240	239
177	45	45
277	26	26

$\lambda = -1{\cdot}8076$ $\log C = 6{\cdot}0685$ $z_e = 100$

(*d*) *Data of Freeman* (*1945*)

Freeman also trapped at Tetney and sampled simultaneously at three heights, though only up to 277 ft. Densities were estimated with much more accuracy than by Hardy & Milne, as wind-speeds appropriate to each height and occasion were used. These data were published as totals over long periods; thus it is possible to use only arithmetic means. Table 2 shows the closeness with which the formula expresses the observed profile.

(*e*) *Data of Glick* (*1939*)

The data considered here were collected over the country round Tallulah, Louisiana, in the Mississippi valley, 80 to 85 ft above sea level; there the land is flat with very many waterways and lakes, forests and also some agricultural areas. In his paper Glick gives total numbers of insects caught for all trapping periods, 1926 to 1931; he does not give the numbers caught in each separate trapping period. Consequently arithmetic means only are possible and in transforming his data, *e.g.* to logarithms, it is the logarithm of a mean based on this total which must be used and not the mean of the logarithms for separate trapping periods as with the Cardington data (p. 491). Thus it is not possible to obtain geometric means.

The total time spent trapping at each height from 20 to 15 000 ft varied considerably, but at 200, 1000, 2000, 3000 and 5000 ft it was maximal, and varied only from 9622 to 10 277 min. Presumably, therefore, sampling at these heights was done more or less on the same occasions, and the observations have been regarded as simultaneous; *i.e.* 10 min were spent at each height over a two-hour period of flight (Glick 1939, p. 82, Fig. 2). The observations at other heights were much less frequent and probably made in the better weather; if so they would be weighted with high densities. At this stage, however, data for heights below 200 and above 5000 ft will not be considered.

Because of ignorance of air-speed and trap area it has not been possible to convert all Glick's figures to the number of insects per unit volume of air (*i.e.* to density). Glick states, however, that the speed of the aircraft was standardized, and he has estimated the average volume of air occupied by one insect at different heights, basing his calculations on the speed and area of the trap and the total catch of all insects for the period 1926 to 1931 (Glick 1939, Table 7). He has also given total numbers caught and total trapping times (Glick, Table 9). Number/10^6 cu. ft and number/10^3 min can thus be found (Table 3, columns 3 and 4). Both number/10^6 cu. ft and number/10^3 min are from the same data; therefore their ratio at each height should be constant and this ratio should be a factor for converting volume to time estimate and vice versa. This enables the two observed estimates (volumetric and time period) to be checked against each other by obtaining a calculated number/10^3 min from observed number/10^6 cu. ft using the conversion ratio. If the ratio is obtained from data at 200 ft (1303 : 148) then calculated and observed figures do not agree (cf. Table 3, columns 4 and 6).

With ratios from 1000, 2000 and 3000 ft (475 : 63, etc.) observed and calculated values do agree except at 200 ft (cf. Table 3, columns 4 and 7).

Similarly number/10^6 cu. ft calculated from number/10^3 min agree (except at 200 ft) only when the conversion factor is obtained at 1000 or more ft (Table 3, columns 4 and 8). This suggests that Glick made an arithmetical error in his data for 200 ft, possibly in his figures for numbers of minutes of flight, and this might account for small discrepancies in fitting Glick's curves to the general formula (see p. 489). I have therefore taken the ratio of number/10^6 cu. ft number/10^3 min for 1000, 2000 and 3000 ft, *i.e.* 0·132632 as a conversion factor for transforming number/10^3 min to number/10^6 cu. ft. Observed and expected values for daytime catches agree closely (Table 4), but there is a consistent error which makes the observed density at 1000 ft smaller than the calculated value.

Table 3. *Estimates of density from Glick's (1939) data*

Height (ft)	Observed			Calculated		
	Volumetric density					
	cu. ft/insect	Insects per 10^6 cu.ft	No./10^3 min	No./10^6 cu. ft Ratio from 1000 ft	No./10^3 min 200 ft	No./10^3 min 1000 ft
200	6 750	148	1303	173	1303	1116
1000	15 902	63	475	63	555	475
2000	30 981	32	241	32	282	241
3000	55 370	18	135	18	158	136
5000	117 540	9	64	8	79	68

The error mentioned above might account for the discrepancy between observed and calculated values at 1000 ft in Table 4. Had the calculated curve been fitted so that observed and calculated densities were made equal at 1000 ft instead of at 200 ft, then the calculated density at 200 ft would be smaller than the observed value there, so following Glick's error. One other possibility, however, is that the percentage error in the estimation of height is likely to be at its greatest at 200 ft.

Table 4 shows that for night-time catches observed and calculated values of density tend to differ considerably at the two highest altitudes (3000 and 5000 ft). This could be attributed to the dispersal processes changing at night with changes in convective turbulence; however, the trapping time at 5000 ft is minimal and the number of insects caught is usually very small indeed. The actual catches are:

	3000 ft	5000 ft		3000 ft	5000 ft
Araneida	6	1	Lepidoptera	2	7
Heteroptera	2	5	Hymenoptera	4	9
Homoptera	34	14	Diptera	62	37
Coleoptera	12	16	All orders	126	104

With total orders and with Diptera the numbers are fairly large and the observed and calculated values in Table 4 agree fairly well, but with the smaller numbers this is not so. A sampling error might, therefore, be responsible for poorly fitting curves at these heights. As with the daytime figures there is a tendency for the calculated values to exceed the observed values. No explanation is offered for this.

Table 4. *Data from Louisiana (Glick 1939)*

Arithmetic mean number of insects/10^6 cu. ft

Height (ft)	Sampling time (min)	Araneida		Diptera		Hymenoptera		Heteroptera		Homoptera		Thysanoptera		Coleoptera		Total all orders	
		Obs.	Calc.	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.
DAYTIME																	
200	10 277	8·1	8·1	66·8	66·8	21·2	21·2	7·2	7·2	19·3	19·3	0·57	0·57	28·8	28·8	172·8	172·8
1000	10 101	4·7	4·4	26·0	25·8	6·7	7·0	2·8	2·7	7·5	9·1	0·28	0·27	6·8	6·2	63·0	70·0
2000	9 767	3·0	2·3	13·9	12·7	3·2	3·1	1·5	1·2	4·9	4·8	0·14	0·14	2·2	2·5	32·0	32·6
3000	10 102	1·3	1·3	7·7	7·7	1·5	1·7	0·7	0·7	3·7	3·0	0·10	0·09	1·3	1·4	17·9	18·6
5000	9 622	0·5	0·5	3·8	3·9	0·8	0·8	0·3	0·3	1·4	1·6	0·04	0·04	0·7	0·6	8·5	8·3
λ		−4·1739		−1·6161		−1·8731		−2·1355		−1·7524		−1·7849		−1·6143		−2·1154	
log C		16·2146		6·6731		6·9456		7·5758		6·8514		5·4249		5·8164		8·9562	
z_e		4 800		800		800		1 200		1 300		1 300		300		1 300	
NIGHT-TIME																	
500	1 664	2·23	2·23	62·81	62·81	8·05	8·05	9·17	9·17	41·53	41·53	8·37	8·37	54·20	53·99		
1000	1 488	1·60	1·38	27·99	27·81	4·19	4·00	4·01	3·79	17·65	19·12	2·76	2·58	10·70	12·39		
2000	1 248	0·74	0·86	13·82	12·34	1·70	1·70	1·28	1·25	9·35	7·19	0·53	0·58	2·76	2·84		
3000	1 225	0·65	0·65	6·71	7·66	0·43	0·98	0·22	0·60	3·68	3·78	0·22	0·22	1·30	1·20		
5000	1 165	0·11	0·46	4·21	4·21	1·02	0·47	0·57	0·22	1·59	1·59	0·80	0·06	1·82	0·40		
λ		−0·6880		−1·1738		−1·5852		−2·1790		−1·9138		−2·9044		−2·1266			
log C		2·2052		4·9661		5·5888		7·4994		7·3598		9·6359		7·4737			
z_e		1		1		400		500		500		500		1			

(*f*) *Data from Cardington (England), 1948, 1950 and 1951*

The country is level for ½ to 3 miles around Cardington and the fields adjacent to the trapping site are pastures, playing fields and agricultural land; half a mile to the north-west the ground rises about 50 ft with many low buildings and falls to its former level about 1 mile further on. Two to three miles to the south and south-east the ground rises to hills (a 250 ft rise) which extend to the south-west, 5 to 6 miles distant. To the north-east, the land is flat for many miles.

Much of the dispersal and distribution of insects, particularly in the lower layers of the air, is probably influenced by the immediate local surroundings such as buildings, ploughed fields or roads, which cause turbulence and convection. Unfortunately it is not possible to compare such details between localities listed here.

In 1948 six tow-nets operating simultaneously at different heights were flown from the cable of a barrage balloon. Opening and closing mechanisms ensured that the nets opened to trap insects only at the appropriate heights and times; this apparatus has been described elsewhere (Johnson & Taylor 1955*b*). The nets themselves are detachable and after trapping were folded with the catch into large tins with a little ether and emptied next day.

In 1948, aphids were the chief concern. The importance of their diurnal flight periodicity in the dispersal process had been appreciated, and trapping periods were therefore as short as possible; *i.e.* of two-hour duration from 07·30 to 09·30, 10·30 to 12·30 and 13·30 to 15·30 h G.M.T., with occasional two-hour periods throughout the evening or night.

The method of estimating aerial density with tow-nets has already been fully discussed (Johnson 1950). The measurement of the mean wind-speed at each height, or its estimation by interpolation or extrapolation is used to assess the amount of air passing through each net during the trapping period (and this quantity is not a simple proportion of wind-speed); the number of insects caught is then standardized to number/10^6 cu. ft of air per trapping period. This is a long, laborious process when six nets with different wind-speeds and catches, flying at different times of day operate over a whole season, and although this density estimate seems to be fairly reliable for the present purpose with wind-speeds generally about 6 m.p.h, the errors are great in calm weather and special consideration of data collected in low wind-speeds would be necessary in a more detailed analysis.

In 1950 and 1951 four suction traps (12 in. aerofoil, exposed cone) were used on a tower and balloon cable up to 1000 ft in the air; these traps segregated the catch into hourly samples and were run usually from 07·30 to 15·30 h G.M.T. The design, operation and accuracy of suction traps has been described in other papers (Johnson & Taylor 1955*a*, *b*, Taylor 1955). The traps used in 1950 and 1951 sampled air at an average rate of 1680 cu. ft air/min ± 10%. This mean rate and the error is appropriate for extreme operational conditions (*i.e.* maximum variation in wind-speed, electrical variation and of differences between individual traps) likely over a long period of several weeks or months. From day to day or within a day such extremes are unlikely and the mean air delivery is then 1793 cu. ft/min ± 4·5%.

Density estimates are obtained directly from the catch in relation to the volumetric flow during the trapping period. Many errors associated with density estimates with tow-nets, as well as the lengthy calculations and the need to measure wind-speed are thus eliminated. However, one error not yet properly assessed is the proportion of insects which escape from the air about to be sampled by being blown by the wind beyond the trap; this proportion should increase with increase of wind-speed and mass of the insect. But although a large error may occur in a density estimate, it is unlikely to affect the general conclusions drawn about the gradient in this paper; for errors due to the difference in wind-speed between lowest and highest traps on any one occasion are relatively small. It is not possible at present to cope with the catches of more than one trap at each height. Therefore sampling errors cannot be given, but they are being investigated.

Table 5. *Means and standard deviations* (σ) *of insect density at Cardington, May-October 1948*

Two-hour trapping periods with tow-nets. Density (χ) = number/10^6 cu. ft

				Arith. mean density			Geom. mean density	
Height (ft)	No. of obs.	Mean $\log_{10}(\chi+1)$	σ	Obs.	σ	Calc.	Obs.	Calc.
APHIDS: 07·30-15·30 h G.M.T.								
50	151	1·49	0·6670	85·1	188·2	90·0	29·6	29·6
250	151	1·18	0·7358	51·3	99·9	43·2	14·1	14·7
500	151	0·93	0·5845	17·7	31·9	22·2	7·6	7·8
1000	147	0·62	0·5186	8·3	20·2	8·8	3·1	3·3
1500	145	0·47	0·4698	5·1	12·5	4·6	1·9	1·8
2000	144	0·31	0·4041	2·8	8·5	2·8	1·0	1·1
		λ			−2·1834		−2·0736	
		$\log C$			7·8472		7·0679	
		z_e			450		450	
INSECTS OTHER THAN APHIDS (INCLUDING SPIDERS): 07·30-15·30 h G.M.T.								
50	151	1·91	0·8192	252·3	418·70	251·6	80·3	80·3
250	151	1·48	0·7271	111·1	262·10	91·6	29·2	28·8
500	151	1·10	0·6657	37·3	86·00	42·9	11·9	13·4
1000	147	0·81	0·6047	16·2	32·18	17·0	5·5	5·2
1500	145	0·58	0·5621	9·6	22·93	9·3	2·8	2·8
2000	144	0·45	0·5138	5·9	13·10	6·0	1·8	1·8
		λ			−1·7186		−1·7429	
		$\log C$			6·5217		6·0840	
		z_e			200		200	
APHIDS: 10·30-12·30 h G.M.T.								
50	54	1·62	0·5395	84·7	152·8	84·7	40·7	40·7
250	54	1·22	0·7383	55·5	125·0	44·5	15·6	16·9
500	54	0·99	0·5328	16·9	19·4	24·2	8·8	8·4
1000	52	0·60	0·4808	6·0	7·6	10·1	3·0	3·5
1500	52	0·50	0·4882	5·7	12·2	5·4	2·2	2·0
2000	53	0·37	0·4061	2·8	4·6	3·3	1·3	1·3
		λ			−2·2417		−1·7227	
		$\log C$			8·1558		5·8769	
		z_e			550		250	

Table 6. *Means and standard deviations (σ) of aphid density from hourly catches at Cardington, 1950 and 1951*

Catches were made in aerofoil (exposed cone) suction traps.
Density $(\chi) = \text{number}/10^6$ cu. ft ± 4·5%.

Height (ft)	No. of obs.	Mean $\log_{10}(\chi+1)$	σ	Arith. mean density			Geom. Mean density	
				Obs.	σ	Calc.	Obs.	Calc.
12 JULY 1950: 11·30-15·30 h G.M.T.								
10	3	2·24	0·2456	195·2	109·57	174·0	175·8	154·6
150	3	1·47	0·3464	37·2	32·16	31·8	29·4	25·8
200	3	1·20	0·4042	21·7	21·47	26·4	15·9	21·2
1000	3	0·97	–	9·3	–	9·3	9·3	7·1
		λ		−0·6495			−0·6831	
		$\log C$		2·9170			2·9006	
		z_e		1			1	
26, 27 AND 31 JULY 1950: 07·30-13·30 h G.M.T.								
10	4	1·85	0·5963	109·2	72·58	105·8	70·9	70·9
150	4	1·51	0·2020	34·9	15·89	32·0	32·2	32·8
500	4	0·97	–	9·3	–	8·5	9·3	9·7
1000	4	1·04	0·1500	11·6	4·65	3·4	11·0	3·4
		λ		−1·5478			−2·1834	
		$\log C$		5·2425			7·3495	
		z_e		110			320	
13 JULY-20 OCTOBER 1950: 08·30-14·30 h G.M.T.								
10	16	1·88	0·4386	107·4	72·47	105·0	76·4	76·4
150	16	1·31	0·2383	29·1	31·26	28·8	20·4	19·8
500	16	0·97	–	9·3	–	9·1	9·3	9·3
		λ		−1·1761			−0·6503	
		$\log C$		4·1910			2·7291	
		z_e		60			10	
16 JULY-24 OCTOBER 1951: 07·30-15·30 h G.M.T.								
10	32	1·98	0·4932	185·3	280·31	174·4	96·5	96·5
50	32	1·53	0·4628	63·3	95·61	67·61	33·7	47·2
250	10	1·38	0·3867	35·3	37·13	25·26	24·1	18·2
500	32	1·07	0·5911	13·1	7·41	16·48	11·7	12·0
		λ		−0·6178			−0·6476	
		$\log C$		2·8850			2·8270	
		z_e		1			10	
3-24 OCTOBER 1951: 09·30-15·30 h G.M.T.								
10	10	2·28	0·4978	349·4	449·43	315·0	189·8	190·0
50	10	1·88	0·4512	127·3	149·33	143·5	75·5	82·4
250	10	1·38	0·3867	35·3	37·13	30·0	23·9	21·8
500	10	10·6	0·2025	13·0	8·76	13·1	11·4	11·4
		λ		−1·3369			−0·9864	
		$\log C$		4·7697			3·7358	
		z_e		40			20	

At Cardington in 1948, when trapping at the six heights simultaneously, often nothing was caught at one or more heights especially during the period 07·30 to 09·30 h G.M.T. All such zeros are included in the data summarized in Table 5; this makes a skew frequency distribution. The use of geometric means, therefore, produces better agreement with the theoretical curves than do arithmetic means. By selecting a trapping period when zero catches were few, this source of error is minimized without the loss of much valuable data; but geometric means still give the better fit. I have not considered the three trapping periods (07·30 to 09·30; 10·30 to 12·30; 13·30 to 15·30 h G.M.T.) separately in this paper, preferring to deal with them when discussing the change in the density-height profile during the day (Johnson 1956*b*), but the mean densities at different heights for these periods fit the general equation for the profile. For the catches made at Cardington in 1950 and 1951 a better fit is in general obtained with geometric than with arithmetic means (Tables 6 and 7).

Table 7. *The single hour when aphids were caught at all heights to 1000 ft. Cardington, 09·30-10·30 h* G.M.T., *25 July 1951*

12 in. aerofoil (exposed cone) suction trap.

Height (ft)	No./10^6 cu. ft	
	Obs.	Calc.
10	65·1	64·9
50	37·2	53·5
500	18·6	16·9
1000	9·3	9·4
λ	−1·0863	
log C	4·3125	
z_e	190	

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SUMMARY

1. Many insect species, perhaps the majority of those flying in rather exposed situations, become dispersed into the upper air above about 100-200 ft. The population in the upper air is not distinct from that flying in the lower layers, since in general, from zero height to some thousands of feet there is a continuous distribution, density diminishing with height in a well-defined profile.

2. This profile may be interpreted in terms of particle diffusion wherein all

individuals are subject to upward and downward diffusion by flight, gravity and turbulence. Such a gradient can be expressed accurately by the formula

$$f(z) = C\ (z+z_e)^{-\lambda}$$

Where $f(z)$ is density at height z,

C is a scale factor depending on population size,

λ is an index of the diffusion process and of the profile,

z_e is a parameter whose significance probably depends on the rate of exchange of insects between air and ground.

This expression may not hold good when the profile is decaying or building up.

3. The empirical derivation of the expression is described and most relevant published data on vertical distribution up to 5000 ft have been satisfactorily fitted to the above expression.

4. This expression for the profile can be integrated to give an estimate of the total numbers of insects in a given zone of air or, within practical limits in the whole atmosphere. λ expresses in a single parameter the relative numbers at different heights; thus the more insects there are in the lower compared with the upper layers of the air, the higher the value of λ will be.

5. The expression is the first step in an analysis of the vertical dispersal process which will be discussed in a later paper in relation to mathematical and physical theories of diffusion.

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Johnson, C. G. (**1956b**). The vertical distribution of aphids in the air and the temperature lapse rate. *Q.J. Roy. Met. Soc.* **83,** 194-201.

Johnson, C. G. & Penman, H. L. (**1951**). Relationship of aphid density to altitude. *Nature, Lond.* **168,** 337-8.

Johnson, C. G. & Taylor, L. R. (**1955a**). The measurement of insect density in the air. *Lab. Practice,* **4,** 187-92, 235-9.

Johnson, C. G. & Taylor, L. R. (**1955b**). The development of large suction traps for airborne insects. *Ann. Appl. Biol.* **43,** 51-61.

Taylor, L. R. (**1955**). The standardization of air-flow in insect suction traps. *Ann. Appl. Biol.* **43,** 390-408.

Wolfenbarger, D. O. (**1946**). Dispersion of small organisms. *Amer. Midl. Nat.* **35,** 1-152.

REVIEWS

BIRD POPULATIONS

L. E. Richdale (1957). *A Population Study of Penguins.* Pp. iii+195; 2 plates; 8 text-figures. Oxford: Clarendon Press. Price 42*s*.

The foundations of this book were laid by a study of the yellow-eyed penguin *Megadyptes antipodes* on breeding areas on the Otago Peninsula, New Zealand, from August 1936 to March 1954. The author has already published one book, *Sexual Behaviour in Penguins*, and a number of papers reporting findings from the earlier years of this long-sustained investigation. This final record of those aspects of it relating to the population problem will not disappoint those acquainted with the earlier work. It contains a well-marshalled assembly of a great mass of data on the yellow-eyed penguin, together with critical summaries of existing knowledge of all other species of Sphenisciformes. The author has studied seven other species himself and so has been well able to evaluate the published data on species not occurring in New Zealand.

The peculiar merits of the penguins studied by Richdale are that they are largely sedentary and come ashore during half the year and can be caught when ashore without too much difficulty. Thus, once he had overcome (by the use of aluminium bands and foot markings together) the difficulty of ensuring that known birds remained marked, he was in a position to compile very detailed records of the lives of several hundred individuals, including almost all the inhabitants of the main study area, comprising a colony of 25 mated pairs in 1940-41, which increased steadily to 82 mated pairs in 1952-53.

After an introductory chapter including a section devoted to 'Explanation of Terms' which defines no less than thirty-two with admirable economy, there follows an account of the pair-bond. Yellow-eyed penguins do not as a rule pair for life, only about three-fifths of the pairs remaining together from one season to the next. A third of the disruptions are due to divorce or separations, caused largely by the tendency to wander shown by younger birds. The investigation of this juvenile wandering is discussed at length in a later chapter. This species has a prolonged adolescence, not reaching full sexual maturity until five years, although nearly half the two-year-old females studied laid eggs and nearly all the three-year-old females bred. Maturity is finally demonstrated by the elimination of wandering as well as the attainment of full fertility. Males mature more slowly than females, very few two-year-olds acquiring mates and three-year-olds also being 'backward'. This is presumably bound up with the fact that older males always outnumber breeding females so that males compete for mates: even males in the age range of 5-13 years, the period of full sexual powers, mostly have to endure at least one season without a mate in seven or eight years. The existence in the community of appreciable numbers of 'aged' birds (over thirteen years old) of slightly impaired capacity provides a situation not often reported in studies of bird populations (although probably existing in other sea-birds).

Juvenile wandering is related to the difficult practical problem of determining the extent of immigration and emigration. Among birds breeding for the first time about half bred where they were hatched and the remainder were immigrants, and this ratio applied also to the total adult population. There is an illuminating discussion of the probability of inbreeding, showing how few opportunities for pairings between different generations are provided even in so sedentary and long-lived a community. No parent-child pairings were found, though nearly one-fifth of the number of brother-sister pairings that might have occurred were detected; most of these were away from the place of hatching.

It is the massive accumulation of details which makes this study so informative, but inevitably a text interspersed with eighty-seven tables does not read very easily, despite the admirable skill of the printers. There are places, too, where the 'documentation' becomes unnecessarily oppressive as, for example, in the treatment of variation in egg size and incubation period, both topics accessory to the main theme. Chapter summaries might have been helpful in ensuring that the author made clear his interpretations as well as his data. This work is going to be cited often on many topics and it is unfortunate that the method of presentation is such that most borrowers will be forced to use their own condensations rather than quotations or paraphrases, with a consequent loss of precision.

Penguin enthusiasts will naturally want to read this book. All other students of animal populations should too, because long-lived species such as penguins provide the equivalent of a slow-motion picture of processes and situations difficult to detect in species with a more rapid turnover. It is difficult to believe that this intricate and fascinating picture of penguin communities is the outcome of 'a spare-time occupation confined largely to week-ends'.

H. BOYD

David Lack (1956). *Swifts in a Tower.* Pp. 239; 10 plates; 24 text-figures. London: Methuen. Price 21*s*.

Scientists are sometimes accused of writing crabbed stuff so that no one can read their works with any pleasure or even understand them without being an expert. All too often the accusation is well founded, though the necessity for terseness in order to satisfy editors of journals is sometimes partly responsible. But this book is as clear a demonstration as one could have that it need not be so. Most of it is a straightforward scientific account of a very large number of hours, spread over ten years, spent observing the swifts by Dr Lack, his wife and his colleagues, though it is here and there enlivened by human touches and apt similes, which would probably not have passed the editor of a journal but add enormously to the reader's enjoyment.

Ornithology is a branch of zoology which it is possible to pursue with very little experience or specialized equipment, and which has therefore been a good deal pursued by amateurs. But there is nothing amateurish here, simple though the equipment used was. Indeed the idea of converting the ventilators in the tower of the Oxford Museum into observation chambers in which the swift could be watched nesting, was one of those strokes of genius which dazzle by their simplicity. As a result the swift must now be one of the best known in its nesting and breeding habits of any of our British birds. One of the most striking things about the story is the very small margin between success and failure in the rearing of the young, and the extent to which the balance is affected by the weather. The uncertainties of this part of the life history and the dangers to which the adults must presumably be exposed in the course of their annual migrations make it seem rather surprising at first sight that their broods should be so small, but when one considers the large number of chironomids which must be required to provide a square meal even for a swift, the necessity demonstrated by Dr Lack to keep the brood within the adults' capacity for providing food is easily understood.

Besides the study of the Oxford colony the book contains much information on the habits and distribution of the other members of the swift family all over the world, a subject on which the author is very learned.

This is a book which must be read by every ornithologist and will be read with enjoyment by many others who have an interest in the problem of animal numbers.

H. C. GILSON

A GUIDE FOR TAXONOMISTS

Edward T. Schenk & John H. McMasters (1957). *Procedure in Taxonomy.* Third edition enlarged and in part re-written by A. Myra Keen and Siemon William Muller. Pp. vii+119. California: Stanford U.P.; London: Oxford U.P. Price 28*s*.

The fourth declaration of the International Commission on Zoological Nomenclature is 'On the need for avoiding intemperate language in discussions on zoological nomenclature'. Anyone who has ever made close acquaintance with this subject will be aware of the need. It should grow less in future years if authors follow the rules and recommendations in the book under review and they will also find it helpful when they come to unravel the tangles of the past. It originated in an article entitled 'Recommendations for the procedure in the description of a new species' and this has probably been changed only because it does not indicate that the scope is restricted to the legal aspect. The reader learns the difference between holotype, paratype, syntype and six more, and is advised how to establish a type of his own; what to include in the way of synonymy, record of repositories of the type material, indications of type locality, and so on in his description of a new species; and where to deposit it. He will find some helpful remarks on the selection of a name and even assistance with spelling and form if his knowledge of Latin is slight, and, unless he has had long experience, he will appreciate particularly the chapter on setting out synonymy. All this is presented in twenty-nine concisely written pages.

There are two and a half pages on the International Commission and the rest of the book is taken up by the appendix which comprises an English version of the *Règles Internationales de la Nomenclature Zoölogique*, the opinions, declarations and directions. There are summaries of the opinions rendered up to 1936 but after that year the Commission took steps to protect its publications by copyright with the result that it is possible to quote only the titles and not the decisions on questions on which opinions have been rendered since. This will be disappointing for the owner of this book though it is something beyond the competence of the authors. Another disappointment will be that little is said about the far-reaching decisions of the 1953 Congress of Zoology at Copenhagen and the reader learns nothing more than where to find Hemming's account which is described as 'an interim Code pending final publication of the definitive Code'. Doubtless the authors have good reasons for waiting for the definitive code and the fact that it has been seen fit to issue a new edition now, although new rules may be expected in a year or two, is a more eloquent testimony to this book than any fair words a reviewer may write.

T. T. MACAN

THE YEAR'S ENTOMOLOGY

E. A. Steinhaus & R. F. Smith (Editors). *Annual Review of Entomology*, Vol. 2, 1957. Pp. viii+407; 10 text-figures. Palo Alto, California; Annual Reviews Inc. Price $7.50.

Only three or four of the twenty articles in this volume will be of direct appeal to readers of this Journal, but many of the others contain matter of some ecological interest. M. E. Solomon reviews the literature of the last 10 years on the Dynamics of Insect Populations (113 refs.) and brings out the immense complexity of situations in nature, the limitations of laboratory studies, and the fact that natural populations are not necessarily being continuously regulated. Comparing the view-points of the two current schools of thought, the one that populations are self-governing systems, the other that they are controlled by extrinsic factors, Solomon suggests that adherence to one or the other may be largely determined by personal experience of a particular type of environment. Thus biotic factors appear important in equable climates whilst in extreme climates, less favourable to insect life, physical factors seem more important in determining numbers. Nevertheless he would hold that in both situations the same principles apply and that density-dependent processes do operate.

C. B. Williams, writing on Insect Migration (62 refs.), summarizes the evidence in the different orders and discusses orientation, the mechanism of which is not yet satisfactorily explained, the 'return flight', and population density in relation to migration. W. G. Wellington, in a plea for The Synoptic Approach to Studies of Insects and Climate (80 refs.) discusses methods of studying the relationship of micro-environments to general weather records and the influence of weather on insect behaviour and population size. M. J. D. White writes on Cytogenetics and Systematic Entomology (87 refs.), F. I. van Emden on The Taxonomic Significance of the Characters of Immature Insects (148 refs.), M. V. Brian on Caste Determination in Social Insects (105 refs.), A. W. Linquist and E. F. Knipling on Recent Advances in Veterinary Entomology (145 refs.), G. E. Bohart on Pollination of Alfalfa and Red Clover (140 refs.) and L. Broadbent on Insecticidal Control of the Spread of Plant Viruses (73 refs.). There are five articles on insecticides.

This book certainly succeeds in the aim set out in Vol. 1 of giving authoritative and concise accounts of subjects of current interest, and will be widely welcomed by entomologists. It is provided with subject and author indices. The editors regret that it was not possible to use alphabetized bibliographies throughout. It is to be hoped that these can be adopted in future volumes, for if authors would arrange references in this way, number them, and cite them by number only in the text (one is generally not interested in who discovered something, but in what has been discovered) then greater convenience and economy of writing would be achieved.

J. H. MUNDIE

AN ITALIAN JOURNAL IN ENGLISH

Selected scientific papers from the Istituto Superiore di Sanità. Vol. 1, pt. I. Pp. 233; 3 coloured and 10 half-tone plates; many text-figures. Rome: Fondazione Emanuele Paterno; English version, Oxford: Blackwell. Price 57*s*. 6*d*.

There are twelve articles, one on cosmic radiation, one on a comparison of photographic and photoelectric methods in absorption spectroscopy, and the rest on insecticides or genetics, mainly those of *Musca* though *Drosophila* has been studied by one of the authors. The reviewer has read three of the articles. The standard is high and the results likely to be important to those engaged in the control of disease. Most ecologists, however, will find them outside their spheres of interest.

It is a little surprising that, though this is a new venture, there is no introduction nor any explanation why an Italian institute has decided to publish its results, or rather some of its results to judge from the title, in English, though the decision is certainly gratifying. It seems hard that the translator should remain anonymous, for he deserves a word of praise. Nor is the name of the editor to be found, though on page 3 where there is a list of the staff of the Institute, the names of the photographers and artists are given.

The print is large, the spacing and illustration lavish. In comparison headings and literature lists are like tin shacks flanking some fine Georgian façade. The authors' names come first in bold capitals and the titles of the articles in bold lower case start immediately after them and run on like a paragraph of letterpress. The reviewer's opinion that this is a parsimonious way of setting up a heading may be due to conservatism, but he is not prepared to concede as much about the references. These, apart from the small print and the crowding together, have three faults. First, they are referred to in the text by the author's name and a serial number. The amount of space saved by this number instead of the more usual date is negligible and the disadvantage is that a reader familiar with the subject and its literature may, for example, easily recognize Sacca (1952) as a paper that he knows, but cannot recognize Sacca (8). Secondly, the titles of the papers are omitted and only the journals given, which is tiresome because the scope of a work is often far from clear when it is mentioned in the text, and the quotation of the title in the reference list may save anyone wishing to pursue the question further both time and trouble. Thirdly, the date is put at the end, where it has to be hunted for, and not after the author's name, where it is immediately obvious. The extra room that titles and a more generous spacing would have taken up could easily have been saved by some editing of the text.

The fifth paper is about the loss of effectiveness of DDT sprayed on to bricks supplied from various parts of the Middle East. When they arrived they were broken; Fig. 1 is a photographic study of broken bricks. They had to be remade and there are three photographs of the process although it is one likely to be familiar to most British readers from childhood or parenthood experiences at the seaside. There are four photographs of the apparatus used to obtain samples of the brick at different depths below the surface, to say nothing of seventeen coloured plates of the surfaces of bricks. One grows less surprised that the photographer but not the editor was named at the beginning. In fairness it must be added that the most extreme example has been selected.

However, though the inclusion of illustrations that could have been dispensed with is bound to excite any British biologist, who must pare his works down to the barest essentials before he starts hawking them round from editor to editor, it is not an important fault. This publication, with its clear layout, its numerous diagrams, some in two colours, and its summaries in English, Italian, French and German, is an important new step in making fresh discoveries known as widely as possible and as such it is to be welcomed.

T. T. MACAN

A LOCAL JUBILEE

Kettering and District Naturalists' Society and Field Club (1956). *The First Fifty Years.* Pp. 134. Kettering: Published by the Society (Hon. Secretary, R. E. Leaton, 11 Wordsworth Rd, Kettering, Northants). Price 10*s*. 6*d*.

The majority of local natural history societies were founded either during the last century or in comparatively recent years. The Kettering and District Society came along in the last fling of the vigorous Victorian interest in local field studies, and so is enabled to celebrate its jubilee in this useful little volume. The Society had a somewhat unusual beginning, in an advertisement in a local evening paper by three enthusiastic naturalists, and rented its first room, in Workhouse Lane (now squeamishly renamed Dryland Street!) Kettering, for the modest sum of a shilling a week.

The principal paper in the collection is 'The Birds of John Clare', by James Fisher, in which 148 species of birds are identified with a greater or less degree of certainty in the poet's writings, 67 of them constituting the earliest known records of the species in the county.

Of more specifically ecological interest is 'The Bird Ecology of a Northamptonshire Woodland', a qualitative study of the birds of a 300-acre stretch of woodland near Corby, by J. R. Launden. F. A. Adams lists the galls found in Northamptonshire by 40 species of Hymenoptera, Coleoptera, Lepidoptera, Diptera, Homoptera and Acari, with the plant on which they were found. Other papers deal with plant ecology of limestone grassland, ironstone workings and lichens.

R. S. R. FITTER

RECORDING NATURE

Eric Simms (1957). *Voices of the Wild.* Pp. 230; 15 plates. London: Putnam. Price 21*s.*

The author succeeded Ludwig Koch in charge of nature recording for the B.B.C. He tells in this book of some of his journeys and vigils with the microphone in places all over the British Isles, with trips to the Camargue and Spain thrown in.

Though not perhaps what most people mean by ecology the book is natural history at its best, and includes much acute observation of birds and mammals from the point of view of their behaviour and especially the sounds they make. The style is plain and without furbelows but graphic, and enough is said about the habits and appearance of nearly all the many species mentioned to retain the interest even of a non-ornithologist. There is an interesting final chapter on recording techniques.

H. C. GILSON

BOOKS RECEIVED

The American Arbacia and other sea urchins. By ETHEL BROWNE HARVEY. Princeton: University Press (London: Oxford University Press). 1956. Price 48*s.*

The Golden Treasury of Natural History. By BERTHA MORRIS PARKER. London: Publicity Products. 1956. Price 22*s.* 6*d.*

Wild America. By R. T. PETERSON and JAS. FISHER. London: Collins. 1956. Price 30*s.*

What is Science? Edited by JAS. R. NEWMAN. London: Gollancz. 1956. Price 21*s.*

Handbook of snakes of the United States and Canada. By A. H. and A. E. WRIGHT. Two volumes. Ithaca: Comstock. 1957. Price $14.75.

The Spirit of the Wild: studies in North American life. By WM. J. LONG. London: Heinemann. 1957. Price 18*s.*

Proceedings of the third Berkeley Symposium on mathematical statistics and probability. Vol. IV. *Contributions to Biology and Problems of Health.* Edited by JERZY NEYMAN. Berkeley: University of California Press. 1957. Price 43*s.* 6*d.*

The life of mammals. By J. Z. YOUNG. Oxford: Clarendon Press. 1957. Price 84*s.*

The Physiology of Fishes. Vol. I. *Metabolism.* Edited by MARGARET E. BROWN. New York: Academic Press. 1957. Price $12.00.

Audubon Western Bird Guide. By RICHARD H. POUGH. New York: Doubleday (sponsored by the Audubon Society). 1957. Price $4.95.

Twentieth-Century Bestiary. Edited by DENNIS FLANAGAN. London: Bell. 1957. Price 13*s.* 6*d.*

ABSTRACTS

The abstracts are edited by Professor L. A. Harvey with the assistance in selecting and abstracting of J. A. Allen, J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, P. D. Gabbutt, N. A. Holme, S. J. Holt, D. Leatherdale, A. Macfadyen, C. Matheson, E. J. Moynahan, Miss E. Nelmes, W. R. Pickering, J. L. Cloudsley-Thompson, G. G. Vickers, Mrs M. Vincent, M. Williamson and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, The University, Exeter.**

Separate copies of the abstracts suitable for mounting on cards can be obtained from **Blackwell Scientific Publications Ltd., 24-25 Broad Street, Oxford,** or through any bookseller; price 5*s*. 6*d*. per annum, post free (issued in May and November). Back numbers of the 'Notices of publications . . .' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s*. for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. FOOD AND FOOD HABITS';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Johnson, A. L. (1957). Seal marking 1956-57. *Nature in Wales*, **3,** 377-381.

154 Seals (82 cows, 65 bulls and 7 undetermined) ringed by the West Wales Field Society from September 1956 to March 1957 inclusive, many of them on Ramsey Island. Seventeen recoveries, 12 locally, 3 from south-west England, one from Eire, and one from the French coast.

(*b*) Fresh Water

Alabaster, J. S., Herbert, D. W. M. & Hemens, J. (1957). The survival of rainbow trout (*Salmo gairdnerii* Richardson) and perch (*Perca fluviatilis* L.) at various concentrations of dissolved oxygen and carbon dioxide. *Ann. Appl. Biol.* **45,** 177-188.

An investigation of the relative importance of dissolved oxygen and carbon dioxide in determining the lethal effect of an environment for rainbow trout and perch. Apparatus was devised to control the concentrations of the gases in a body of water.

Davis, R. A. (1956). The coypu. *Agriculture*, **63,** 127-129.

Although its range has increased in recent years, actual numbers are not much greater. Habitat requirements are too circumscribed for it to become ubiquitous.

Jackson, D. J. (1956). Observations on water-beetles during drought. *Ent. Mon. Mag.* **92,** 154-155.

Discusses habits and means of survival of both flying and flightless water-beetles after six weeks' drought in Inverness-shire.

Kettle, D. S. (1956). Rainfall and larval density of *Culicoides impunctatus* Goetghebuer (Diptera: Ceratopogonidae). *Proc. R. Ent. Soc. Lond.* (A) **31,** 173-177.

Close correlation shown between larval density in autumn and rainfall during the preceding period of adult activity.

Lansbury, I. (1956). Further observations on the ecology of *Cymatia coleoptrata* (Fabricius) (Hemipt.—Heteroptera, Corixidae) in southern England. *Entomologist*, **89,** 188-195.

Maps the vice-comital distribution in Great Britain and compares the ecological conditions in ponds in north Somerset, east Kent, southern Essex and southern Hertfordshire in which *C. coleoptrata* is common or dominant. Depth and pH varied considerably, but optima were 3-4 ft. and 7·5-8·5, respectively. In all the ponds there was a dense vertical growth of submerged vegetation, of which *Ceratophyllum* was commonest, but *Myriophyllum* also appeared to be very important. (See 1955, *Entomologist*, **88,** 66-67 and abstract in 1955, *J. Anim. Ecol.* **24,** 473.)

Weerekoon, A. C. J. (1956). Studies on the biology of Loch Lomond. 1. The benthos of Auchentullich Bay. *Ceylon J. Sci.* (Sect. C, Fisheries). **7,** 1-94.

Describes bathymetric and seasonal distribution of the bottom fauna, discussing quantitative sampling methods and rapid extraction techniques.

Weerekoon, A. C. J. (1956). Studies on the biology of Loch Lomond. 2. The repopulation of McDougall Bank. *Ceylon J. Sci.* (Sect. C, Fisheries), **7,** 95-133.

Discusses repopulation of a submerged bank at least 450 m from shore by larvae of flying insects. Shows that eggs do not reach it and postulates current transport of planktonic larval phases and selective settlement.

(*c*) Land

Barnes, H. F. (1956). Gall midges as pests of farm crops (2). *Agriculture*, **63,** 336-339.

Damage caused by and control of various species is discussed.

Brian, M. V. (**1956**). The natural density of *Myrmica rubra* and associated ants in west Scotland. *Insectes Sociaux*, **3**, 473-487.

Traces changes in ant populations during overgrowth of a glade in spruce-pine woodland, mainly through colony elimination. Statistical demonstration of aggregation of four ant species, each species, however, showing either random distribution or overdispersal.

Broadbent, L. (**1956**). *Brassica* virus diseases. *Agriculture*, **63**, 69-72.

Spread by aphids whose numbers depend largely upon the weather.

Bryce, D. (**1956**). Notes on the life-history of *Tipula cheethami* Edw. (Dipt., Tipulidae). *Ent. Mon. Mag.* **92**, 104-106.

Notes on the habitat requirements and food of the larvae of this semi-aquatic species, with a description of the larva.

Chant, D. A. (**1956**). Predacious spiders in orchards in south-eastern England. *J. Hort. Sci.* **31**, 35-46.

Lists spiders found in sprayed and unsprayed orchards in Kent and Essex, with a discussion on their relative abundance, food preferences, and notes on the habits of spiders belonging to the families Theridiidae and Linyphiidae.

Charles, W. N. (**1956**). The effects of a vole plague in the Carron Valley, Stirlingshire. *Scot. For.* **10**, 201-204.

Vegetation changes ; damage outside the forest ; sampling. Up to 75% (locally 100%) of plantation trees up to 15 years old were damaged or killed.

Crooke, M. & Bevan, D. (**1957**). Note on the first British occurrence of *Ips cembrae* Heer (Col. Scolytidae). *Forestry*, **30**, 21-28.

In 1955 this larch bark beetle was discovered in 29 localities in Moray, Nairn, Banff and Inverness, the first British records for this species. It is assumed that *I. cembrae* entered the country in post-war shipments of German timber and has persisted in small numbers until the damage to woodlands caused by the gale of 1953 provided favourable conditions for its increase. Twig tunnelling by the adult beetles produces crown pruning, and may kill established trees.

Dobson, R. M. (**1956**). A note on the relative abundance of flea beetles (*Phyllotreta* Stephens and *Psylloides* Berthold) on different cruciferous crops. *J. Hort. Sci.* **31**, 291-294.

Examination of flea-beetle populations suggests that small cruciferous plants are more severely attacked than are large ones. Host preferences are indicated for *Phyllotreta undulata*, *P. atra*, *P. nemorum*, *P. nigripes* and *P. cruciferae*.

Hunter, W. R. (**1957**). Mollusca from limestone in Skye, with special reference to *Pyramidula rupestris* (Draparnaud). *J. Conch.* **24**, 171-173.

The effect on the distribution of snails of isolated outcrops of limestone.

Hussey, N. W. (**1956**). The extent of seed-loss in Douglas fir caused by *Megastigmus*. *Scot. For.* **10**, 191-197.

Megastigmus spermotrophus the Douglas fir seedfly, frequently attacks Douglas fir seed very seriously. Factors affecting survival of eggs, larvae and pupae ; survey of extent of crop infection in successive years. Predation by small rodents is important. A useful ecological study.

Irvine, T. W. (**1956**). Larch bark beetle. *Scot. For.* **10**, 218-219.

A short note about the eight-toothed larch bark beetle, *Ips cembrae*. Can attack trees only slightly reduced in vigour, and even kill them.

Lockley, R. M. (**1957**). Grassholm: some facts and a legend. *Nature in Wales*, **3**, 382-388.

Gives a summary of the history of the gannet on Grassholm and discusses a stone-walled enclosure, which is suggested to have been a gannet-catching corral.

Mackenzie, J. M. D. (**1956**). Tree-creepers using nest-boxes and other artificial nest-sites. *Scot. Nat.* **68,** 84-91.

Experiments in Scotland : 45 out of 70 bark-type sites were used, and 20 out of over 500 boxes. Instructions how to make a tree-creeper box.

Mackenzie, J. M. D. (**1956**). Parasitism of bird nests by bumble bees. *Scot. Nat.* **68,** 114-115.

Fifty instances of bird nests in nest-boxes taken over by bees, probably all *Bombus lucorum*, also eight wasps' nests, usually in empty boxes.

Milne, B. S. (**1956**). A report on the bird population of Beddington sewage farm, 1954-55. *Lond. Bird Rep.* **20,** 39-54.

Describes habits and habitats of breeding, feeding and wintering birds and discusses weight of various factors adverse to breeding populations.

Oates, F. B. (**1956**). Menace of the mole. *Agriculture*, **63,** 79-82.

Although essentially insectivorous the mole is a menace to agriculture because of its habit of tunnelling under growing crops. The mole spends most of its time in its complex system of feeding runs where its appetite for insects and worms is insatiable. It has few natural enemies and is distasteful to some predators. Badgers become adept at catching moles.

Singh, M. P. & Kevan, D. K. McE. (**1956**). Notes on three common British species of Agrotid moth. 1. Longevity and oviposition. *Ent. Rec.* **68,** 233-235.

The result of laboratory investigations on *Triphaena pronuba*, *Agrotis segetum* and *Amathes c-nigrum*.

Southwood, T. R. E. & Scudder, G. G. E. (**1956**). The bionomics and immature stages of the thistle lace bugs (*Tingis ampliata* H.-S. and *T. cardui* L.; Hem., Tingidae). *Trans. Soc. Brit. Ent.* **12** (3), 93-112.

Host plants, life histories, larval structure, key to larvae, wax secretion, geographical distribution and distribution on host plants.

Stokes, B. S. (**1957**). Observations and experiments on the hessian fly (*Mayetiola destructor* Say). *Ann. Appl. Biol.* **45,** 122-132.

The hessian fly was recorded on couch grass (*Agropyron repens*), but wheat was the preferred host. More midges were reared from young plants than from mature ones. There were three main flights per year, with some overlapping of the generations. Other hosts are listed.

Thompson, H. V. (**1956**). Myxomatosis: a survey. *Agriculture*, **63,** 51-57.

There are now no really heavy rabbit infections in England although some moderate ones or small pockets exist. Myxomatosis is not the complete answer to all rabbit problems and follow-up measures are necessary.

Thompson, J. L. Cloudsley- (**1956**). The effect of rock cover on the diurnal range of microclimatic conditions. *Entomologist*, **89,** 213-215.

Comparative measurements on, above and under rocks in sun and shade show the microclimate under the rocks to be much the most equable. Detailed data given.

Thompson, J. L. Cloudsley- & Sankey, J. H. P. (**1956**). Some aspects of the fauna of the district around Juniper Hall, Mickleham, Surrey—III. *Ent. Mon. Mag.* **92,** 132-134.

Includes a list of invertebrates collected on the banks of the river Mole, where the relative humidity was 89·2 % at ground level and averaged 80 % on trees at a height of 1·5 m, and others of invertebrates collected on acid and base-rich soils, in which the approximate number per sq. m of each is indicated. (See 1953, *Ent. Mon. Mag.* **89,** 284-286 and abstract in 1955, *J. Anim. Ecol.* **24,** 214.)

Williams, C. B., Singh, B. P. & El Ziady, S. (**1956**). An investigation into the possible effects of moonlight on the activity of insects in the field. *Proc. R. Ent. Soc. Lond.* (A), **31**, 135-144.

Extensive trapping data reveal no regular lunar cycle in numbers of insects caught.

Wiltshire, E. P. (**1956**). Studies in the geography of Lepidoptera VI. A new suggestion regarding the history of the swallow-tail butterfly in the British Isles. *Ent. Rec.* **68**, 257-260.

In Baghdad, the principal food plant of *Papilio machaon* is cultivated rue (*Ruta*), on which its survival depends, and it is suggested that the virtual disappearance of this butterfly in Britain within historic times may be correlated with the disappearance of rue from gardens, where it was formerly cultivated for medicinal purposes.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Acton, A. B. (**1956**). The identification and distribution of the larvae of some species of *Chironomus* (Diptera.) *Proc. R. Ent. Soc. Lond.* (A), **31**, 161-164.

Discusses identification of chironomid larvae by use of the band pattern in giant chromosomes.

Alam, S. M. (**1956**). The taxonomy of some British aphelinid parasites (Hymenoptera) of scale insects (Coccoidea). *Trans. R. Ent. Soc. Lond.* **108**, 357-384.

Provides a key to some genera of the Aphelinidae.

Barnes, H. (**1955**). Underwater television and research in marine biology, bottom topography and geology. *Sonderd. Deutsch. Hydrograph. Z.* **8**, 213-236.

Describes, with examples, the use of underwater television for observing and estimating quantitatively both bottom-living and planktonic organisms. Difficulties and failures are discussed.

Boyd, H. J. (**1957**). Gulls on Lundy, 1947-56. *Rep., Lundy Fld. Soc.* **10** (1956), 26-32.

The breeding populations of *Larus argentatus*, *L. fuscus*, *L. marinus* and *Rissa tridactyla* are tending to decline, probably due to mortality of adults away from the island.

Chiswell, J. B. (**1956**). A taxonomic account of the last instar larvae of some British Tipulinae (Diptera: Tipulidae). *Trans. R. Ent. Soc. Lond.* **108**, 409-484.

Describes and illustrates the last instar larvae of thirty-six British species and provides a key to the species.

Davidson, A. (**1956**). A method of counting Ephemeropteran eggs. *Ent. Mon. Mag.* **92**, 109.

Method, devised for *Cloëon simile*; the eggs are counted in a standard Sedgwick-Rafter plankton-counting cell after being stained and sieved.

Dobson, R. M. & Lofty, J. R. (**1956**). A simple cage for confining small insects during experimental exposure to fumigants, etc. *Ent. Mon. Mag.* **92**, 157-158.

A cage of two brass washers, to each of which fine phosphor-bronze gauze is soldered, held face to face by means of a rubber band.

Evans, G. O. & Hyatt, K. H. (**1956**). British mites of the genus *Pachylaelaps* Berlese (Gamasina-Pachylaelaptidae). *Ent. Mon. Mag.* **92**, 118-129.

Keys to the females of the seven known British species and the males of four of them. *P. multidentatus* and *P. undulatus* are both described as new from females collected from decaying wood in Hertfordshire, the latter also found in pond refuse in Middlesex. *P. tesselatus* is recorded for the first time in Britain, from Essex.

Fonseca, E. C. M. d'Assis- (**1956**). A review of the British subfamilies and genera of the family Muscidae (Diptera). *Trans. Soc. Brit. Ent.* **12** (4), 113-128.

Tables of subfamilies and genera.

Laughton, A. S. (**1957**). Photography of the deep-sea floor. *Discovery*, **18**, 59-62.

Describes the construction of a camera and illumination unit for photographing the deep-sea bed, developed in England at the National Institute of Oceanography and used in 1956 from R.R.S. *Discovery II*.

Leston, D. (**1956**). A key to larvae of the families of British Hemiptera-Heteroptera. *Entomologist*, **89**, 223-231.

Locket, G. H. (**1956**). An effective top-light for use with a microscope. *Ent. Mon. Mag.* **92**, 131.

Diagrams and brief instructions for an arrangement devised for the examination of spiders in spirit, but probably also of use to entomologists.

Mackereth, J. C. (**1956**). Taxonomy of the larvae of British species of the sub-family Glossosomatinae (Trichoptera). *Proc. R. Ent. Soc. Lond.* (A), **31**, 167-172.

A key to the genera *Glossosoma* and *Agapetus*.

Southwood, T. R. E. (**1956**). A key to determine the instar of an Heteropterous larva. *Entomologist*, **89**, 220-222.

This key was developed principally for larvae of Cimicomorpha, but has proved satisfactory for a wide range of species. It is not entirely reliable for Pentatomid larvae or for the first and second instars of most families, and cannot be used for larvae with only four instars.

van Emden, H. F. (**1956**). Morphology and identification of the British larvae of the genus *Elater* (Col., Elateridae). *Ent. Mon. Mag.* **92**, 167-193.

Includes descriptions and habitats for the larvae of the 14 species recognized, with a key to 13 of them.

Waterston, A. R. (**1956**). *Corixa striata* (L.) sensu Jaczewski, 1924 (Hem., Corixidae) in East Kent. *Ent. Mon. Mag.* **92**, 142-143.

C. striata is recorded in Britain for the first time and a key is given for its separation from *C. dorsalis*.

3. PARASITES

Allan, R. M. (**1956**). A study of the populations of the rabbit flea *Spilopsyllus cuniculi* (Dale) on the wild rabbit *Oryctolagus cuniculus* in north-east Scotland. *Proc. R. Ent. Soc. Lond.* (A), **31**, 145-152.

A tentative life history with notes on adult habits and sex distribution in the rabbit.

Bezant, E. T. (**1956**). *Gelis micrurus* Förster (Hym., Ichneumonidae) parasitizing a Lycosid spider egg-sac. *Ent. Mon. Mag.* **92**, 106.

Two males and four females emerged from the egg sac of a female of *Lycosa pullata* caught in Surrey in June 1955.

Brown, E. B. (**1957**). Lucerne stem eelworm. A serious threat to lucerne growing. *Agriculture*, **63**, 517-520.

Dunn, E. (**1956**). Cereal root eelworm. *Scot. Agric.* **36**, 146-148.

Since the war there has been a considerable increase in the number of poor oat crops, sometimes total failures, and these have been caused by the cereal root eelworm, *Heterodera major* Schmidt. Life-cycle and hosts are listed. Chemical control is uneconomic, and crop rotation is the only procedure of present value.

Jackson, D. J. (**1956**). Notes on hymenopterous parasitoids bred from the eggs of Dytiscidae in Fife. *J. Soc. Brit. Ent.* **5**, 144-149.

A number of species of Chalcidoidea were bred from eggs collected from these localities.

Scott, R. E. (1957). Some internal parasites from an Iceland redwing. *Brit. Birds,* **50,** 122-123.

A dead Iceland redwing (*Turdus musicus coburni*) in Surrey in February 1956 contained *Dilepis undula, Porrocaecum ensicaudatum, Prosthorhynchus transversus, Anomotaenia constricta.* The last two are first records for redwings in Britain.

Smith, K. M. (1956). Virus diseases of insects: their use in biological control. *Agriculture,* **63,** 271-275.

Some kinds of virus disease offer possibilities of control, e.g. that causing granulosis disease of the caterpillars of white butterflies.

Southwood, T. R. E. (1956). Records of Mymaridae (Hym) parasitizing the eggs of certain Heteroptera. *Ent. Mon. Mag.* **92,** 162.

Polynema gracile emerged from an egg of *Nabis limbatus* (apparently its first record from a Nabid), and *Enaesius agilis* from eggs of *Leptoptera dolabrata.*

4. FOOD AND FOOD HABITS

Parmenter, L. (1956). Beetles visiting the flowers of dogwood, *Cornus sanguinea* L. *Ent. Rec.* **68,** 243-244.

Five species, additional to those previously recorded at flowers of dogwood, are listed.

Parmenter, L. (1956). Flies and their selection of the flowers they visit. *Ent. Rec.* **68,** 242-243.

The numbers of each of 10 Syrphids, a Tachinid and a Muscid that were observed on adjoining patches, approximately equal in size, of *Achillea millefolium, Hypochaeris radicata* and *Centaurea nigra* during half an hour.

Woodroffe, G. E. (1956). Some insects and mites associated with bat-roosts, with a discussion of the feeding habits of the Cheyletids (Acarina). *Ent. Mon. Mag.* **92,** 138-141.

The fauna of roosts of *Pipistrellus pipistrellus* resembles that of dry birds' nests (see 1953, *Bull. Ent. Res.* **44,** 739-772 and abstract in 1955, *J. Anim, Ecol.* **24,** 225) and is composed of scavengers (many of which are species associated with stored products), species predaceous on them, and ectoparasites of the bats. Some evidence was obtained that predatory Cheyletids on occasion suck the blood of the bats.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Andrewes, C. H. (1956). *Helocera delecta* Mg. and other uncommon Diptera in the Isle of Wight. *J. Soc. Brit. Ent.* **5,** 164-165.

A Tachinid fly previously recorded only from Cambridge and Dorset.

Ashe, G. H. (1956). Some Coleoptera new to the Devon list taken in 1955. *Ent. Mon. Mag.* **92,** 166.

Records of four species.

Benson, R. B. (1956). Sawflies (Hym., Symphyta) at Malham Tarn. *Ent. Mon. Mag.* **92,** 166.

Fenella monilicornis, Nematus tuberculatus, N. apicifrons and *N. similator* all recorded for the first time from England.

Blezard, E. (1956). The mammals of Lakeland. *Oryx,* **3,** 334-338.

Red, roe and fallow deer all present in places. A few pine martens still surviving. Badgers and brown hares increasing, a few mountain hares. Rabbits reviving. Red squirrel and dormouse decreasing. Several records of grey squirrel. Seven species of bat recorded.

Collin, J. E. (**1956**). Some new British Borboridae (Diptera). *J. Soc. Brit. Ent.* **5,** 172-178.

Notes on thirteen species new to the British list.

Collingwood, C. A. (**1956**). Aberrations in British ants of the genus *Formica*. *J. Soc. Brit. Ent.* **5,** 193-196.

A colony of *F. lemani* at Ambergate, Derbyshire, contained some 50 pseudogynes, 150 workers and 6 queens.

Collingwood, C. A. (**1956**). Distribution of ants allied to *Formica fusca* L. and *F. rufa* L. in Britain. *Entomologist*, **89,** 291-294.

A discussion of the known distribution of *F. fusca*, *F. lemani*, *F. cunicularia*, *F. aquilonia*, *F. lugubris* and *F. rufa*.

Collingwood, C. A. (**1957**). Myrmecophilous beetles in the Midlands. *Ent. Rec.* **69,** 9-14.

Many new county records for beetles associated with ants, mostly *Formica rufa* and *F. lugubris*, and the relative abundance of some in different counties is shown in a table. The Staphylinid, *Thiasophila angulata* was the most abundant and comprised over 30 % of the total.

Collingwood, C. A. & Satchell, J. E. (**1956**). Ants of the south Lake District. *J. Soc. Brit. Ent.* **5,** 159-164.

The distribution of 17 species of ants is discussed and the relative abundance of the more common species in various habitats compared.

Colyer, C. N. (**1956**). Phorid flies, damaging cultivated mushrooms, *Megaselia plurispinosa* (Lundbeck 1920) (Diptera, Phoridae) a synonym of *Megaselia* (*M.*) *halterata* (Wood 1910). *J. Soc. Brit. Ent.* **5,** 166-171.

Davidson, A. (**1956**). *Dirhagus pygmaeus* F. (Col., Eucnemidae) new to Scotland. *Ent. Mon. Mag.* **92,** 149.

In a dry, decaying birch log in western Ross-shire.

de Kock, L. L. (**1956**). The pilot whale stranding on the Orkney island of Westray, 1955. *Scot. Nat.* **68,** 63-70.

Notes on the stranding of 67 *Globicephala melaena* in March 1955.

Edwards, J. (**1956**). Diptera new to the Staffordshire county list. *Ent. Rec.* **68,** 275.

Tephritis bardanae on burdock and *Stratiomys potamida*.

Fonseca, E. C. M. d'Assis- (**1957**). Some interesting and uncommon Diptera from East Kent, including a new species of *Phaonia* (Muscidae). *Ent. Rec.* **69,** 14-18.

The new species is *P. umbraticola*.

Fordham, W. H. (**1956**). Melanic grey squirrels at Ashwell. *Trans. Herts. Nat. Hist. Soc.* **24,** 198.

French, R. A. (**1956**). Migration records, 1955. *Entomologist*, **89,** 139-145, 174-180.

A survey of the movements of migrant Lepidoptera recorded in and round Britain in 1955, with a table showing the abundance and range of regular migrants in 1954.

George, R. S. (**1956**). *Rhadinopsylla* (*Actenophthalmus*) *integella integella* J. & R. (Siphonaptera: Hystrichopsyllidae), a flea new to the British Isles. *Entomologist*, **89,** 201-202.

Lists 15 species and subspecies of fleas taken on small mammals in Scotland, including a number of new county records. *R. integella integella* is recorded on *Microtus agrostis* in Angus and *Clethrionomys glareolus* in Perthshire.

Hager, P. D. (1956). Melanic grey squirrels near Berkhamsted. *Trans. Herts. Nat. Hist. Soc.* **24,** 198.

Hardy, D. E. (1956). The Lepidoptera of Fair Isle. *Entomologist,* **89,** 261-269.

The species collected in a survey during 16 August-2 September 1955 are listed and their abundance indicated. Many were darker in colour than the mainland stocks. A population survey of *Cerapteryx graminis* during 20 August-1 September established that the moths rapidly disperse throughout the island and then die or fail to be attracted to light, and the populations are greatly affected by weather conditions.

Harper, G. W. (1957). The Macrolepidoptera of Inverness-shire—Newtonmore district. Supplement. *Ent. Rec.* **69,** 52.

Three species new to the district. (See 1955, *Ent. Rec.* **67,** 39-40 and abstract in 1955, *J. Anim. Ecol.* **24,** 491.)

Harrison, J. W. Heslop- (1956). Further observations on the Lepidoptera of the Outer Hebrides. *Entomologist,* **89,** 285-290.

Includes several new records for the Outer Hebrides, Lewis and Harris.

Hincks, W. D. (1956). Notes on three species of micro-Hymenoptera from Charterhouse Pools. *J. Soc. Brit. Ent.* **5,** 150-152.

Records *Lymaenon alecto, Inostemma boscii* and *I. spinulosum* from Charterhouse Pools, Somerset.

Kevan, D. K. McE. (1956). The known distribution of British Orthopteroids, fourth supplement. *J. Soc. Brit. Ent.* **5,** 187-192.

Records and corrections.

Lansbury, I. (1956). A list of the aquatic and semi-aquatic Hemiptera-Heteroptera recorded from Hertfordshire, with notes on species found in the Barnet area. *Trans. Herts. Nat. Hist. Soc.* **24,** 192-196.

Lansbury, I. F. M. (1956). Check list of the genera of the aquatic and semi-aquatic Hemiptera-Heteroptera of the British Isles. *Ent. Mon. Mag.* **92,** 150-153.

Leston, D. (1956). The British species of *Sigara* (*Sigara*) Fabricus (Hem., Corixidae). *J. Soc. Brit. Ent.* **5,** 153-158.

Sigara striata occurs in south-east Britain whereas *S. dorsalis* is widely distributed.

Massee, A. M. (1956). Hemiptera-Heteroptera associated with fruits and hops. *J. Soc. Brit. Ent.* **5,** 179-186.

All the species recorded on fruit are common and well known with the exception of *Xylocoridea brevipennis,* found under loose bark, and *Lygus visicola* which feeds on mistletoe. Only five species can be described as pests and these are not very important.

Hincks, W. D. (1956). Notes on the Elateridae (Col.) of the 'British List'. *J. Soc. Brit. Ent.* **5,** 197-198.

Seven invalid names are discussed.

Rae, B. B. & Wilson, E. (1956). Rare and exotic fishes recorded in Scotland during 1955. *Scot. Nat.* **68,** 92-109.

Notes on 44 species ; Ray's bream, black bream and three other species were probably aided by a strong autumn influx of oceanic water into the North Sea.

Riggall, E. C. (1956). Notes on Lincolnshire Coleoptera. *Trans. Lincs. Nat. Un.* **14,** 14-29.

An extensive review of the beetles of Lincolnshire.

Sage, B. L. (1956). Notes on some Coleoptera from Pembrokeshire. *Ent. Rec.* **68,** 312.
Includes five species new to the county.

Scudder, G. G. E. (1957). The Heteroptera in Wales. *Nature in Wales,* **3,** 394-396.
Of 503 species of Heteroptera known to inhabit the British Isles, 326 have been recorded in Wales. *Stollia aenea* from Cardiganshire is known elsewhere in the British Isles only from Bedford, Kent, Sussex and Hants.

Shaw, S. (1956). *Telenomus punctatissimus* (Ratzeburg) (Hymen., Scelionidae) new to Britain. *J. Soc. Brit. Ent.* **5,** 165-166.
Recorded from Cheshire, Westmorland, Norfolk, Hampshire and Merioneth.

Shaw, S. (1956). On the occurrence of *Hylecoetus dermestoides* (L.) and *Lymexylon navale* (L.) (Col., Lymexylidae) in Lancashire and Cheshire. *J. Soc. Brit. Ent.* **5,** 172.
There are two old records of *H. dermestoides* from Lancs., but this rare beetle is more widely distributed in Cheshire. *L. navale* has not been recorded in either county during the present century.

Sheals, J. G. (1956). Notes on a collection of soil Acari. *Ent. Mon. Mag.* **92,** 99-103.
Eulohmannia ribagai and *Pergamasus misellus* recorded for the first time in Britain; the former common under *Agrostis-Fescue* pasture in Argyll and the latter in cultivated plots on old grassland on heavy loam at Glasgow. Two new species described as *Digamasellus reticulatus* and *Rhodacarellus epigynialis* common at both places, and at Glasgow, respectively.

Smith, K. G. V. (1956). Concluding notes on the Lepidoptera of Shropshire. *Entomologist,* **89,** 167-173.
Records, with localities, dates and, occasionally, food plants, for a further 151 species. (See also 1954, *Entomologist,* **87,** 107-111 and abstract in 1955, *J. Anim. Ecol.* **24,** 244.)

Smith, K. G. V. (1956). *Sciomyza annulipes* Zett., an addition to the list of British Sciomyzidae (Dipt.). *Ent. Mon. Mag.* **92,** 156.
Recorded from Oxfordshire, Buckinghamshire and Herefordshire.

Stratton, L. W. (1956). The Mollusca of the Malham area. *J. Conchol.* **24,** 111-138.
A comprehensive account of the terrestrial and aquatic habitats of Mollusca in the neighbourhood of Malham, Yorks., with three maps.

Thompson, J. L. Cloudsley- (1956). Notes on Arachnida, 27.—The fauna of a Cotswold limestone wall. *Ent. Mon. Mag.* **92,** 75.
The fauna of this dry stone wall, containing no soil or debris, in August comprised numerous wood-lice (*Porcellio spinicornis* and, in smaller numbers, *P. scaber* and *Oniscus asellus*); *Textrix denticula* and a few immature spiders of two other species; numerous snails (*Pyramidula rupestris*); a few winged Dipterous and Homopterous insects; and *Petrobius* sp.

Thompson, J. L. Cloudsley- (1956). Notes on Arachnida, 28.—Biological observations and records. *Ent. Mon. Mag.* **92,** 193.
Includes several new county records. *Cheiridium museorum,* from bats' dung in a dry attic, survived for almost two months in a tube without food or moisture, whereas *Roncus lubricus,* from fallen leaves, died within a day.

Walls, R. C. (1956). Ayrshire rookeries. *Scot. Nat.* **68, 110-113.**
A survey of the whole county showed 25,851 nests in 126 rookeries.

Whitaker, B. (1957). A summary of work on some breeding birds, 1947-56. *Rep. Lundy Fld. Soc.* **10** (1956), 48-53.
Number of breeding pairs of fulmar, cormorant, shag, oyster-catcher, lapwing, kittiwake, razorbill, guillemot and puffin.

Williams, C. B., Common, I. F. B., French, R. A., Muspratt, V. & Williams, M. C. (1956). Observations on the migration of insects in the Pyrenees in the autumn of 1953. *Trans. R. Ent. Soc. Lond.* **148,** 385-407.

Southward movements of many Lepidoptera and Diptera influenced by sunshine, rather than air temperature, and by land contours. No evidence of wind influence.

6. STUDIES ON BEHAVIOUR

Hudson, F. L. (1957). Robin's nest of unusual construction. *Brit. Birds,* **50,** 124.

A nest in dead grass on the ground was completely domed and approached by a tunnel about five inches long, as smooth as the nest and lined with oak leaves.

Jeffrey, B. & Wallace, D. I. M. (1956). Communal display of pied wagtails. *Brit. Birds,* **49,** 454-456.

A note illustrated with sketches on a flock of pied wagtails observed in October. The birds were grouped in a rough ellipse, and the males displayed, making short hovering flights, aerial chases, and attempts at ground display, the whole performance reminiscent of a black grouse lek.

Lovell, R. E. (1957). Blackbird feeding brood of dunnocks. *Brit. Birds,* **50,** 123-124.

A male blackbird fed a brood of dunnocks in a nest four feet from that of his incubating mate. When his own young hatched he fed them as usual.

Thorpe, W. H. (1956). Records of the development of original and unusual feeding methods by wild passerine birds. *Brit. Birds,* **49,** 389-395.

A blue-tit learnt to wind up a suspended perch on its string to reach fat. Five species which do not normally feed in a hanging posture or use the feet in feeding, including a robin and house-sparrow, learnt to hang on vertical and horizontal strings and feed in an inverted position. The habit may be learnt by observation of another bird, even of a different species.

Whalley, P. E. S. & Wotton, M. J. (1957). Terns nesting underground. *Brit. Birds,* **50,** 121-122.

Nests of four terns (*Sterna hirundo* or *S. macrura*) with eggs, concealed in burrows up to one foot from the entrance in thick turf on the Skerries, Anglesey, in a colony deserted owing to predation by carrion crows and gulls.

7. REPORTS OF ORGANIZATIONS

Oxford Ornithological Society (1957). Report of the Oxford Ornithological Society on the birds of Oxfordshire and Berkshire, 1955. 40 pp.

Includes the usual systematic list, arrival and departure of migrants and report on birds ringed during the year, with a special note on the status of some less common birds in Wytham Wood (Berks).

BRITISH ECOLOGICAL SOCIETY

THE WINTER AND ANNUAL GENERAL MEETINGS

7-8 January 1957

By kind permission of the Zoological Society of London, the Winter Meeting, 1957, was held in their Meeting Room in Regent's Park. A very large number of members was present, the attendance reaching well over 150 on the second day.

Three papers were delivered during the afternoon of 7 January beginning at 2.15 p.m., with Dr. J. Warren Wilson's account of 'Microclimatic control of the distribution of species in late snow areas'. Illustrating his points with coloured slides, Dr. Wilson showed that the winter snow of arctic lands melts especially late each year in certain places; primarily in small hollows in the ground where deep drifts have formed. In these 'late snow areas' special vegetation types occur. At Jan Mayen Island they are arranged in concentric zones: around the edge where snow-lie is brief the vegetation is poor; with later snow-lie the vegetation becomes increasingly rich up to an 'optimum'; and beyond this point towards the centre of the area very late snow-lie brings poorer growth or even bare ground. The enrichment of growth is a result of the reduced wind speeds in these hollows; the central impoverishment arises from restriction of the growing season by excessively late-lying snow.

Local conditions of shelter from wind within late snow areas interact with altitude, so that similar vegetation may occur in the sheltered parts of a late snow area on high ground, and in a more exposed position at low altitude.

Comparing sites at any particular level in the lower ranges of altitude, late snow-lie is associated with the occurrence of low-arctic species since it results from sheltered conditions; but at higher levels where it results more from the lowering of mean temperature, late snow-lie is associated rather with the occurrence of high-arctic species.

Plant growth at Jan Mayen is also limited by nitrogen deficiency. But this effect reinforces the relationships described above, for soil nitrogen levels show the same changes as vegetational richness in relation to duration of snow-lie. This is because the soil micro-organisms which fix nitrogen depend for their activity on the organic substrates provided by dead plants. Counts show that micro-organism numbers are correlated with soil nitrogen content and vegetational richness; and so with shelter from wind. Thus wind speed – determined by microtopography – has ultimate control over the distribution of vegetation types in late snow areas and, indeed, generally at Jan Mayen.

It can be shown that wind speeds are reduced in the shelter of late snow areas, and that plants grow more rapidly here than in exposed positions, given the same soil. This control by wind of plant growth is probably exerted through a cooling effect. Wind disturbs the air, so that the layers near the ground (where arctic plants grow) which become warmed by the insolated soil are cooled by admixture of colder air from higher layers. Also, wind has a direct cooling effect on insolated leaves. As a result of these two effects, leaves exposed to wind may be several degrees cooler than sheltered leaves; and differences of even a fraction of a degree are important to plants in the Arctic, for they are especially sensitive to temperature conditions.

Attention was drawn in the discussion following this paper to the presence of disseminules of various species in the debris on the snow, to the occurrence of small areas exceptionally rich in soil animals, and to the possibility of explaining some of the floristic differences between Jan Mayen and west Greenland in terms of the influence on the latter of a more continental type of climate. Professor G. C. Varley, Mr. A. Macfadyen and Dr. A. S. Watt took part.

In the next talk, on the use of cobalt thiocyanate papers for the estimation of humidity, Mr. M. E. Solomon referred to some of the difficulties in measuring environmental air humidity, and discussed the suitability of the cobalt paper method. A piece of impregnated paper is exposed for an hour or two to the humidity which is to be measured, then immersed in oil (liquid paraffin), mounted on white opal glass, and matched against colour standards. The colours are blue at low humidities, pink at high, with violet shades between. Cobalt papers can be used in small spaces, such as burrows or crevices, and are especially useful where there is layering or a gradient of humidity, as in the vicinity of a stem or leaf, or near the soil, or in a humidity-choice or gradient apparatus. They can be inserted into sites which would be inaccessible to most methods. Disadvantages are the rather long exposure period and the fairly low level of accuracy.

Following methods he had described in 1945, a number of ecologists had used either cobalt chloride or cobalt thiocyanate papers in field investigations, and Mr. Solomon referred to some examples.

Ready-made cobalt thiocyanate paper and coloured glass standards were now available from the manufacturers, which made this method much more convenient than before. The speaker presented tables showing the amounts of error to which the method is liable. Estimates could be kept within 5 per cent of the tone value at the higher humidity levels, and within 10 per cent at most of the lower humidities.

Questions about details of the method, its employment and its accuracy as compared with other methods were asked by Professor G. C. Varley, Dr. C. H. Gimingham, Dr. A. J. Rutter, Mr. A. Macfadyen and Dr. E. W. Jones.

Concluding the session, Mr. T. O. Pritchard spoke on 'A contribution to the genecology of weeds; work in progress on *Euphorbia cyparissias*'.

Mr. Pritchard pointed out that establishment and spread of a weed species is largely dependent on efficient methods of reproduction and is often favoured by self-pollination, apomixis and vegetative reproduction. With reference to the evolutionary origin of species and races of a 'weedy' nature, he suggested that selection of already aggressive biotypes may play a part, while favourable characters may also be brought together by introgression from closely related species. Hybridization coupled with polyploidy has played a major role in the origin of some species which have become weeds.

Euphorbia cyparissias is a native of Europe introduced into North America where it has become a serious weed of pastures, especially in eastern Canada. Two cytological forms have been discovered there – a male-sterile diploid ($2n = 20$) which is an escaped garden ornamental with no seed production, and a fertile tetraploid ($2n = 40$). Both forms can reproduce vegetatively by means of rhizomes. The tetraploid may be distinguished by the significantly larger area of its epidermal cells. A fertile diploid is unknown in Canada. An examination of British material indicated a similar situation here, except that the garden sterile diploid has not escaped and, apparently, all the wild plants in Britain are tetraploid and fertile. No fertile diploid form is known in Britain. Pollen grains were also measured and their contents examined. By this method, the hitherto unknown fertile diploid was located in France. It has, however, a very restricted range compared with the tetraploid, which extends east to Russia, north to Scandinavia and Britain.

Preliminary observations have indicated obvious differences in the field behaviour of the tetraploid and fertile diploid. The tetraploid is very aggressive and it grows successfully in tall-grass communities; it reproduces vegetatively by means of rhizomes and produces a large number of seeds as well; it is shade-tolerant. The fertile diploid which was examined at Fontainebleau does not reproduce vegetatively or only very slightly; it cannot compete with grasses; it is much less shade-tolerant than the tetraploid.

The cytology and breeding behaviour of the three forms of *E. cyparissias* and the related *E. esula* were discussed. Meiotic division is regular in the sterile and fertile diploid and the tetraploid *E. cyparissias*. The chromosome count of $2n = 60$ obtained for *E. esula* and the fact that this species crosses freely with the tetraploid *E. cyparissias* has presented an interesting complex for analysis.

It was suggested in conclusion that the superior reproductive capacity of the tetraploid, with its seed as well as vegetative methods of reproduction, has aided its spread at the expense of the, presumably, parental diploid. Furthermore, polyploidy may also have been accompanied by physiological changes in the species enabling the tetraploid to tolerate a greater range of ecological conditions.

The position of the sterile diploid is still obscure; it is of less interest in this context, being an ornamental probably originating through selection by man.

Professor G. C. Varley, Professor D. H. Valentine and Dr. E. W. Jones referred to the capacity for vegetative reproduction possessed by the tetraploid type and its persistence and aggressiveness. Mr. Pritchard suggested that while aggressive in some of its European stations, more extensive habitats were open to it in Canada where it had become a pernicious weed. Others taking part in the discussion were Dr. G. C. Evans, Dr. J. F. Hope-Simpson and Mr. H. C. Gilson.

The meeting was concluded with tea at 4.30 p.m. A soirée was held in the Fellows' Restaurant of the Zoological Society during the evening, beginning with an informal dinner at 7.30 p.m. This was attended by about 60 members and was greatly enjoyed by all present, who spent the remainder of the evening in profitable conversation.

THE ANNUAL GENERAL MEETING

The 38th Annual General Meeting of the Society began at 10 a.m. on the following morning, 8 January. The following are the (unconfirmed) Minutes of this meeting.

MINUTES OF 38TH ANNUAL GENERAL MEETING

The President, Professor G. C. Varley, took the chair in the Meeting Room of the Zoological Society of London, Regent's Park, at 10 a.m.

(1) The Minutes of the 37th Annual General Meeting, having appeared in *J. Ecol.*, **44**, 2, 640, and being due to appear in *J. Anim. Ecol.*, **24**, 2, were taken as read and were accepted.

(2) The Report of the Honorary Secretaries for the year 1956 was read by Dr. C. H. Gimingham, as follows:

Report of the Honorary Secretaries

The 37th Annual General Meeting of the Society was held in the Department of Botany, Oxford University, at 10 a.m. on 5 January 1956, following a soirée on the previous evening when exhibits were on view and coloured slides of the vegetation of New Zealand and Tasmania were shown by Professor Gordon.

An account of the business meeting, at which the President, Professor Varley, was in the chair, has appeared in *J. Ecol.*, **44**, 2, 640, and will appear in *J. Anim. Ecol.*, **24**, 2.

The remainder of the day was devoted to a series of papers concerned with ecological-genetical problems in plant and animal populations, introduced by Dr. W. B. Turrill, who was followed by Professor D. H. Valentine, Professor C. D. Darlington, Dr. E. B. Ford and Captain C. R. P. Diver. The discussions following these papers indicated that this was a subject commanding widespread interest among members. Papers by Mr. I. H. Rorison, Mr. C. H. Fernando and Mr. J. K. Bates were given on the following morning. The Society is grateful to Professor Darlington and members of his Department for their hospitality. Visitors to Oxford were denied the pleasure of sight-seeing by dense fog but were perhaps the better able to appreciate the academic atmosphere within the precincts of Queen's College.

On 27 and 28 March a two-day symposium on the subject of 'Production' was held in the rooms of the Nature Conservancy, London. This meeting was attended by a large number of members, who heard and discussed papers by Dr. J. D. Ovington, Mr. J. A. Gibb, Dr. F. H. Whitehead, Professor W. H. Pearsall and Dr. E. Gorham, Mr. A. Macfadyen, Mr. J. Corlett, Dr. J. H. Mundie, Mr. E. D. Le Cren, Mr. C. W. R. Spedding, Dr. R. E. Hughes and Mr. A. D. Bradshaw. Estimations of 'stock', 'production' and 'crop' in a variety of plant and animal populations ranging from forest stands to freshwater and sea fisheries were presented. This resulted in a fruitful survey which, we understand, has provided members with fertile ideas for application in related fields. The Society's thanks are extended to the Director-General of the Nature Conservancy for accommodating this meeting.

The Summer Meeting was held in the Lake District, with headquarters at The Ferry House, Far Sawrey, from 13-17 July. Excursions were made to Esthwaite North Fen, habitats in Windermere, Coniston Old Man, the Sunbiggin Tarn area, Roudsea and Witherslack woods and the Merlewood Research Station of the Nature Conservancy. With one notable exception the weather was favourable and a variety of interesting habitats was seen. An informal dinner was held at Grange on the penultimate evening. Our warmest thanks for hospitality are due to the Freshwater Biological Association and Mr. H. C. Gilson, and the Nature Conservancy and Dr. V. M. Conway, and to the other helpers, especially to Mr. E. D. Le Cren, for their painstaking work in arranging the meeting.

A Joint Meeting with the Botanical Society of the British Isles was held in Southampton from 22 to 24 September at which members were guests of the Botanical Society on the first day and the British Ecological Society extended a reciprocal invitation on the final day, when papers by Mr. C. E. Hubbard, Miss E. M. Uren, Mrs. P. A. Caldwell, Mr. P. J. Goodman, Dr. D. S. Ranwell, Mr. R. E. Hall, Mr. J. B. Ford and Mr. S. K. Eltringham were read, five of which formed a symposium on *Spartina*. On the Sunday, which fell between these two meetings, members of both Societies took part in an excursion to the New Forest where groups were conducted on a general ecological tour of the proposed Denny Nature Reserve, an inspection of habitats noted for interesting plants, and a survey of entomological habitats. Professors Raymont and Williams and members of their staffs who acted as hosts and guides, and Dr. Lambert, as local organizer, earned the gratitude of members for a delightful visit, the enjoyment of which was enhanced by an outstandingly fine week-end.

Early in the year the Secretaries sent a circular to members asking for suggestions concerning suitable subjects for discussion at meetings of the Society, offers of papers and other comments. They are most grateful for the large response to this questionnaire, which has provided them with a basis upon which to prepare programmes for the Society's meetings for some while to come. In planning meetings the Secretaries try to arrange a varied programme with a fair balance between botanical and zoological papers that will provide good contact between ecologists working in different fields and serve to emphasize the unity of the subject, yet also provide opportunities for the intensive discussion of specialized subjects and individual contributions. They apologize in advance to members whose offers or suggestions cannot be followed up in the immediate future.

During the year the two parts of the *Journal of Ecology*, Volume **44**, have appeared. No. 1 has 319 pages and contains 14 original papers, 13 book reviews and 4 Biological Flora accounts. The second part, containing 393 pages, includes 15 original papers, 9 reviews, Biological Flora accounts of 5 species, the List of Members and accounts of meetings of the Society in 1955, and of the Annual General Meeting in January 1956.

The parts of the Biological Flora published in this volume were: *Holcus mollis* L., by J. D. Ovington and G. Scurfield; *Carex flacca* Schreb., by F. J. Taylor; *Vaccinium myrtillus* L., by J. C. Ritchie; *Saxifraga oppositifolia* L., by V. Jones and P. W. Richards; *Helianthemum* (the genus), *H. canum* (L.) Baumg., *H. chamaecistus* Mill., and *H. apenninum* (L.) Mill., by M. C. F. Proctor; *Silene nutans* L., by F. N. Hepper; and *Impatiens parviflora* DC., by D. E. Coombe.

At the present time, owing to delays caused by the printers' dispute early in the year, only No. 1 of Volume **25** of the *Journal of Animal Ecology* has appeared. This has 216 pages and contains 12 original papers, reviews of 6 books, 27 pages of abstracts and an account of the 1955 Summer Meeting.

In order to deal efficiently with the increasing business connected with the Journals the Council has formed a 'Standing Committee on Publications'. This committee has been able to consider in detail several important problems and make recommendations to the Council. As the sales of back-numbers of the Journals, and especially sets and runs, are a valuable source of income, both the Committee and the Council have thought it important to maintain stocks of back-numbers and have initiated a programme of reprinting to fill gaps in the series of recent volumes of both Journals. Some of this reprinting will be financed from income but it will also be necessary to draw on capital, though the Council are of the opinion that this change in investment is a sound policy. The Council have also authorized the continuation of a slightly larger-sized *Journal of Animal Ecology* and, in future, the publication of the *Journal of Ecology* in three parts to an annual volume, in order that all suitable material offered for the Journals may be published without undue delay. All these changes, together with increased costs, have necessitated increases in the prices of the Journals to non-members and a proposal to increase the membership subscription.

Membership of the Society continues to increase at the most satisfactory rate of about 50 per year, and stands now at 987 compared with 934 at the start of 1956. Of this total, 183 take both Journals, 516 take the *Journal of Ecology* only, 271 the *Journal of Animal Ecology*, 15 are Associate Members and 2 are Honorary Associates. New members elected during the year numbered 83, the loss through resignations and deaths being 30. It can confidently be expected, therefore, that membership will pass the 1000 mark in 1957, the forty-fifth year in the life of the Society.

The Council has met four times to conduct its regular business of electing members, authorizing plans for future meetings, receiving the suggestions of the Committee on Publications, etc. The President represented the Society at the International Entomological Congress in Montreal and Dr. V. M. Conway was the Society's delegate to the meeting of the International Union for the Conservation of Nature in Edinburgh.

The Secretaries wish again to thank those organizations and departments who have been hosts or good friends to us during the past year, and also those individuals who have assisted the Secretaries in organizing meetings and running the Society and done much of the harder work for them. In conclusion the Secretaries report that the Society prospers and grows and that 1956 has been a year of vigorous and successful activity.

C. H. GIMINGHAM
E. D. LE CREN
31 December 1956 *Honorary Secretaries*

On the proposal of Mr. H. C. Gilson, the Report was adopted.

(3) The provisional report of the Hon. Treasurers was presented by Mr. V. S. Summerhayes. Owing to delays in the completion of financial transactions caused by the change of publisher for the Society's Journals and the printers' dispute in 1956, only a very general estimate of the position at the end of the year could be given. In spite of a record income from subscriptions, the working expenses and especially the cost of producing the Journals had risen to such an extent that a deficit on the year of about £1000 was expected. The completed accounts would be presented to the Society in 1957 and printed in both Journals.

Mr. Summerhayes proposed renewal of the grants of £10 to the Freshwater Biological Association and £2 2*s*. to the British Committee for International Nature Conservation. This was seconded by Dr. M. W. Holdgate, who proposed reappointment of the Society's auditors, Messrs. Ryland, Clift & Co.

(4) Changes in Rules 2, 4, 7, 8a, 8b, 10c and 14, were proposed by the Council, having the objects of (*a*) clarifying the practice of giving members of long standing who resign from the Society on their retirement an Honorary Associateship for life, (*b*) to allow the election of more than one honorary editor for each of the Journals, and (*c*) to provide for an increase in Membership Subscription from 1958.

After a short discussion the new rules were approved by the meeting. [The Constitution and Rules of the Society, incorporating those newly adopted, are printed in full following the account of this meeting.]

(5) Proceeding to the election of Officers and Council for 1957, the following were elected:

Vice-President: J. B. CRAGG
Hon. Secretaries: C. H. GIMINGHAM, E. D. LE CREN
Hon. Editors: (*Journal of Ecology*): P. W. RICHARDS, D. E. COOMBE
(*Journal of Animal Ecology*): H. C. GILSON

On the election of a new editor for the *Journal of Ecology*, Professor A. R. Clapham referred to Dr. H. Godwin's resignation from this office, which marked the end of a long period of active service to the Society, both as Secretary and Editor, characterized by devotion and efficiency which had earned the gratitude of all members. Professor Clapham regretted that Dr. Godwin was not present in person to receive the thanks of the Society, and proposed that a letter should be sent to express them. This was received with acclamation.

Members of Council were elected as follows:

D. J. Crisp } To retire in 1961
M. W. Holdgate }
C. D. Pigott }
H. V. Thompson }
P. Greig-Smith (To retire in 1958)
J. E. Satchell (To retire in 1959)

(6) *Reports of the Honorary Editors*

Mr. H. C. Gilson referred to the causes of delay which had resulted in No. 2 of Volume **24** of the *Journal of Animal Ecology* not appearing before the end of 1956 (see Secretaries' Report). He also announced that a satisfactory form of binding for reprints had been agreed with the publishers. It was hoped by somewhat increasing the size of the parts to reduce the time-lag between acceptance of a paper and its appearance.

Dr. D. E. Coombe spoke of the decision to produce three parts of the *Journal of Ecology* per annual volume, so that similar delays in the appearance of papers in this Journal could be reduced. He appealed for conciseness on the part of all authors, an appeal which was emphasized by several speakers. Professor Pearsall proposed and Mr. J. A. Svendsen seconded that Council should consider the possibility of setting some limit to the length of papers.

(7) Professor P. W. Richards presented the report of the Hon. Editors of the Biological Flora. Following the resignation of Dr. H. Godwin as one of the editors, Dr. D. E. Coombe had been appointed by Council as one of the editors, and their number had been increased to four by the appointment of Dr. C. D. Pigott. The rate at which contributions was being submitted was still low, but it was hoped that contributors would make every effort to raise it. A revised schedule for contributors was being prepared, and discussions were proceeding on the best type of distribution map to be used in future accounts.

After a break for coffee, Professor G. C. Varley began his Presidential Address at 11.30 a.m., speaking on 'Ecology as an Experimental Science'.

This address will be printed in full in both Journals and consequently no summary appears here.

Three papers occupied the afternoon. Mr. P. Greig-Smith discussed 'The interpretation of pattern in vegetation', pointing out that non-randomness of distribution of individuals may be due to two causes: (*a*) The occurrence of one individual in a sample increases the probability of occurrence of further individuals. This results usually from features of reproductive behaviour. (*b*) The Poisson parameter varies over the area examined. Although this dual causation was pointed out by Clapham in 1932, attempts at interpretation of non-randomness have concentrated on the former cause. These have usually taken the form of fitting field data to modifications of the Poisson series based on assumptions about reproductive behaviour. Results have been disappointing for two reasons: (*a*) The size of quadrat used places an arbitrary limit on the area subject to supposed reproductive effects. (*b*) The effects of variation in environmental factors are ignored.

Pattern may be defined as departure from randomness. The following working hypothesis of its significance is suggested. If all environmental factors are within the limits of tolerance for a species, random distribution will result. If one or few factors transgress these limits, distribution of the species will follow the distribution of values of these influencing factors which are themselves unlikely to be random, and non-random distribution will result. The scale of pattern will correspond to the scale of pattern in the influencing factors.

The study of pattern by examining variance of measures of vegetation in units of increasing size, arranged either as a grid or along transects, is suggested. In interpretation allowance must be made for reproductive or morphological pattern. Correlation of scale of pattern with that of the influencing factor may be illustrated by K. A. Kershaw's data for *Agrostis tenuis* in reverting upland pasture. Non-morphological pattern in *A. tenuis* corresponds closely to the pattern of soil depth.

There is a tendency for non-morphological pattern to disappear as a species becomes stable.

Data for stages in developing secondary rain forest illustrate this. This suggests a possible test for stability of vegetation. Attainment of stability may be explained in terms of spread from pioneer individuals and of spread of conditions more favourable to the species. There is some evidence that pattern may sometimes not disappear until a species is dying out, e.g. *Ammophila arenaria*. Such cases are difficult to account for but are, perhaps, due to the development of uniformly unfavourable conditions.

Dr. J. G. Skellam and Dr. A. J. Rutter were among those questioning Mr. Greig-Smith on aspects of the theory and applications of the method described.

Mr. E. Broadhead, speaking on 'An ecological study of mixed species populations exploiting a common resource', referred to the Psocoptera as ecologically the most important of the animals grazing upon the lichen and algal flora of the bark of trees. They are extremely abundant on larch at many localities in the Pennine hills. Of the 22 species living on larch, 9 are abundant and of these 7 have the same food requirements, i.e. *Pleurococcus* and fungal spores, little or no lichen being taken. These, living together on the same trees, form a dense population in which the species are interspersed, their ecological requirements being closely similar. The remaining 2 abundant species are largely restricted to the lichen-covered dead branches of larch, although in the laboratory they will oviposit as freely on *Pleurococcus* as on lichen and readily feed on *Pleurococcus* if lichen is scarce. Preference experiments, in which the insects are given the choice between *Pleurococcus* and lichen, indicate that feeding preferences account for the observed distribution in the field to a considerable extent, if not entirely.

The two lichenophilous species are of interest in that one of them grazes the whole of the lichen, whereas the other feeds on the apothecia alone, which are evidently the only parts of the lichen not containing lichen acid. The second appears, therefore, to be incompletely adapted to its ecological niche.

Sampling of populations at various altitudes above sea level showed that climate affects the various species differently. Mr. Broadhead suggested that climate exerts its influence through its effects upon the food supply, the damper conditions in the hills promoting a more rapid turnover of food. At the higher altitudes, where both living twigs carrying *Pleurococcus* and dead twigs with lichen were abundant, the total psocid populations were 12/foot on the former and 9/foot on the latter. In lowland sites where lichen was present only in small amounts only 1 lichenophilous species was present and this not abundant. The proportions in which the *Pleurococcus* species occurred could be related to the fact that 2 of them feed in the early summer while the other 4 feed later. These findings contribute to the solution of the general problem of the ways in which these mixed populations exploiting the same food supply manage to maintain themselves.

Professor G. C. Varley, commenting that this was an example of a type of ecological research in which – as he had indicated in his Presidential Address – he had great personal interest, initiated a discussion in which Dr. T. T. Macan, Dr. T. B. Reynoldson, Mr. E. D. Le Cren and Mr. M. E. Solomon took part. In answer to questions concerning fluctuations in population numbers, and the influences of predators and parasites, Mr. Broadhead outlined work in progress bearing on these topics.

Mr. J. L. Harper, joint author of the final paper with Mr. J. W. Ludwig, spoke on 'The influence of slope and aspect on the growth of plants'. A full account of the work reported has appeared in Volume **45** of the *Journal of Ecology* and consequently no summary appears here.

Professor G. C. Varley, Mr. H. C. Gilson, Mr. J. G. Skellam, Mr. M. E. Solomon, Dr. A. S. Thomas, Professor O. W. Richards, Dr. E. W. Jones and Mr. J. A. Svendsen took part in the discussion.

In closing the meeting the President thanked the Zoological Society of London for their hospitality and the excellent facilities provided in their rooms for a large and successful meeting.

LIST OF MEMBERS AND ASSOCIATES

(1 April 1957)

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